

PLEISTOCENE RADIOMETRIC GEOCHRONOLOGY AND VERTEBRATE PALEONTOLOGY IN MÉXICO: OVERVIEW AND CRITICAL APPRAISAL¹

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ABSTRACT. The combined radiometric and paleontologic approach drove a qualitative leap in understanding Earth's geologic history and evolution, yet it is still not widely used in México in spite of its early start. In order to stimulate others to apply this fruitful approach, and thus to contribute to better comprehension of México's Quaternary biotic and geologic make and evolution, here we report 21 Pleistocene sites with dated vertebrate-bearing units where such an approach was applied; their space/time distribution is quite uneven, leaving whole regions, morphotectonic provinces, and geochronologic intervals little studied or unstudied. The sites occur only in five of the 11 existing morphotectonic provinces, as follows: Northwestern Plains and Sierras, one Rancholabrean; Sierra Madre Oriental, two Rancholabrean; Trans-Mexican Volcanic Belt, 14 Rancholabrean; Sierra Madre del Sur, two Rancholabrean; and Sierra Madre de Chiapas, two Irvingtonian. No dated sites have been reported for the following provinces: Baja California Peninsula, Sierra Madre Occidental, Chihuahua-Coahuila Plateaus and Ranges, Central Plateau, Gulf Coastal Plain, and Yucatan Platform.

Analysis of the 21 sites treated here discloses the need to describe or revise their lithostratigraphic settings. Nonetheless they are of prime importance for understanding the regional Quaternary environmental change (climatic and otherwise, including timing, extent, and biotic impact). The mammal assemblages from these sites belong to three chronofaunas: Irvingtonian (three sites), Early Rancholabrean (one site), and very Late Rancholabrean (Wisconsinan, 17 sites).

From the beginning to the end of the Pleistocene the fauna underwent a profound change, drastically modifying its taxonomic composition, its biogeographic distribution, and its entire physiognomy with strong trends toward losing meso- and megabaryc taxa by taxonomic depauperation (through selective extinction and/or emigration) and biogeographic shuffling. Thus, the Holocene fauna is an impoverished version of its Pleistocene counterpart.

Finally, during this epoch our own species appears in México. In fact, some of the oldest records of humans in the American continent, based on direct dating of human skeletal material, are from México.

RESUMEN. El enfoque radio-isotópico/paleontológico combinado impulsó un salto cualitativo en el entendimiento de la historia y evolución de la Tierra, empero no se utiliza ampliamente en México, a pesar de su temprano inicio. Con el propósito de estimular a otros en el empleo de este enfoque, y contribuir así a un mejor entendimiento del Cuaternario, se reportan aquí reportan 21 sitios con unidades fechadas que portan vertebrados, donde se empleó este enfoque; su distribución espacio/temporal es dispareja quedando regiones/provincias morfotectónicas y/o intervalos geocronológicos poco o nada estudiados. Los sitios yacen sólo en cinco de las once provincias morfotectónicas existentes, como se muestra a continuación: Sierras y Planicies del Noroeste (NW), 1 Rancholabreano. Sierra Madre Oriental (SMOr), 2 Rancholabreanos. Faja Volcánica Transmexicana (TMVB), 1 Irvingtoniano y 13 Rancholabreanos. Sierra Madre del Sur (SMS), 2 Rancholabreanos. Sierra Madre de Chiapas (SMCh), 2 Irvingtonianos. No se han reportado este tipo de sitios en estas provincias: Península de Baja California (BCP), Sierra Madre Occidental (SMOc), Mesetas y Sierras de Chihuahua-Coahuila (CH-CO), Altiplanicie Central (CeP), Planicie Costera del Golfo Costal (GCP), y Plataforma de Yucatán (YP).

El análisis de los 21 sitios aquí considerados, evidencia la necesidad de describir o revisar su marco litoestratigráfico; a pesar de ello, son de gran importancia para entender el cambio ambiental del Cuaternario (climático y de otro tipo, incluyendo cronología, alcance e impacto biótico). Sus ensambles mamíferianos pertenecen a tres cronofaunas: Irvingtoniana (tres registros) y Rancholabreana (un registro temprano y 17 muy tardíos Wisconsinanos).

En este período, la fauna sufrió un cambio profundo a lo largo del continuo tempo/espacial, modificando drásticamente su constitución taxonómica, distribución biogeográfica y su propia fisonomía, con una fuerte tendencia hacia la pérdida de taxa meso- y megabáricos, empobrecimiento taxonómico (mediante extinción/expatriación) y rearreglo biogeográfico.

Es así que la fauna holocénica es apenas una versión empobrecida de su contraparte pleistocénica. Finalmente, durante esta época, apareció nuestra propia especie en México; de hecho algunos de los registros humanos más antiguos del Continente Americano, basados en fechamiento directo (de material esquelético humano), son de México.

INTRODUCTION

Paleontology, particularly vertebrate paleontology, benefitted immensely from the advent of radiocarbon dating at affordable prices that occurred

in the early 1950s, allowing calibration of the Quaternary Period, which in turn made possible a more precise long-range correlation of geologic events in marine and terrestrial stratigraphic sequences across distant regions and continents.

The application of radiometric dating techniques started early in México with the pioneering effort of Arnold and Libby (1950) on the Cuicuilco site—disclosing human occupation in the Basin of México's southern part as early as 2422 ± 250 years BP—and on remains of the famous Tepexpan Man (4430 ± 350 to 3800 ± 450 years BP). A major advance was the establishment in 1975 of the Radiocarbon Laboratory at the Instituto Nacional de Antropología e Historia (INAH) in México City. This is chiefly devoted to dating archaeolog-

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ically significant sites, which frequently include vertebrate remains, thereby providing ages measured in units of the sidereal time system that we use in our everyday life. The biochronological dating afforded by the fossils themselves enhances precise correlation of sites and vertebrate faunas across the country, places time brackets on climatic events such as changes in temperature and/or humidity, and facilitates the study of biotic succession and faunal turnover at specific sites. These facts are of great archaeological and paleontologic significance.

Unquestionably, the INAH has led the effort to radiometrically date significant archaeological sites in México. A subsequent welcome addition was the foundation in 2004 of the Laboratorio Universitario de Radiocarbono, a radiocarbon dating facility shared by the Instituto de Geología, the Instituto de Geología Geofísica, and the Instituto de Investigaciones Antropológicas, Universidad Nacional Autónoma de México, also in México City.

Radiometric dating of Quaternary sites in México has been primarily focused on solving archaeological questions rather than on vertebrate paleontological problems; however, both disciplines share common cognitive areas and so a great deal of paleontologically significant information has resulted from this effort. For instance, two sites in the Sierra Madre Oriental morphometric province (MP) that yield large and diverse mammal faunas were ^{14}C dated: San Josecito Cave, Nuevo León (Arroyo-Cabrales and Johnson, 1995), and El Cedral, San Luis Potosí (Lorenzo and Mirambell, 1986a), the latter also yielding bonfire charcoal, an indirect evidence of humans in central México. Numerous sites that lie in the Trans-Mexican Volcanic Belt's eastern part were dated, for example, Tlapacoya (González et al., 2003), Tepexpan (Lamb et al., 2009), and Santa Lucía, Estado de México (Arroyo-Cabrales et al., 2004); Peñon III, Distrito Federal, now Ciudad de México (Mercer et al., 2003); and Valsequillo, Puebla (González et al., 2001). The dating of other sites discovered while doing geologic work has enhanced their interpretation, for example, Punta de Llano (Ferrusquía-Villafranca, 1996) and Chiapa de Corzo, Chiapas (Ferrusquía-Villafranca and McDowell, 1991). Other sites, though not bearing human remains or cultural records, were nonetheless dated, because of their large and interesting vertebrate fauna, for example, Térapa, Sonora (Mead et al., 2006).

This overview shows the fruitful results of combining radiometric dating and paleontologic research in México. This helps to better understand this country's vertebrate faunistic evolution, which in turn has a strong bearing in understanding Quaternary climate change and the dramatic physiognomic change of the mammal fauna across Pleistocene time and the Pleistocene/Holocene boundary.

METHODS

An exhaustive bibliographic search was undertaken for sites that have radiometrically dated lithostratigraphic units with vertebrate fossil assemblages or are stratigraphically related to such vertebrate-bearing units, thereby furnishing constraints on the assemblage age and providing minimum/maximum time limits (Table 1 and Fig. 1). The dates were obtained from coal zones, charcoal remains, carbonized plant remains (excluding wood), carbonized wood fragments, and collagen-bearing bone fragments.

From this search, we detected 21 sites across the country from which a reliable analysis can be made. The sites are plotted in Figure 1, a map of the morphotectonic provinces of México (Ferrusquía-Villafranca et al., 2010). The geological/paleontological significance of the sites could be better perceived on a morphotectonic provinces map than on a political-division or state map in which the state boundaries are quite artificial and frequently cut across geologic features.

The morphotectonic provinces include Baja California Peninsula (BCP), Northwestern Plains and Sierras (NW), Sierra Madre

Occidental (SMOc), Chihuahua–Coahuila Plateaus and Ranges (CHCO), Sierra Madre Oriental (SMOr), Gulf Coastal Plain (GCP), Central Plateau (CeP), Trans-Mexican Volcanic Belt (TMVB), Sierra Madre del Sur (SMS), Sierra Madre de Chiapas (CHI), and Yucatan Platform (YPL).

SUMMARY OF SITES INFORMATION PRESENTED AND DISCUSSED

In Table 1, the sites are listed in eight topically grouped columns that treat the following aspects: geographic, geologic, radiometric, and paleontologic-geochronologic aspects.

Geographic–Geologic Aspect

The first column indicates the morphotectonic province and state for each site. The sites are listed consecutively from north to south and from west to east. Within the text the sites are described and discussed in geochronologic order from oldest to youngest. To avoid any confusion, each site is properly named and numbered in the text. A particular site may include a single locality or a cluster of spatially close localities that are designated areas. The chief references, both radiometric and paleontological, are also given (bracketed number after the site name), and spelled out as footnotes.

The second column provides the fossil-bearing unit name from which radiometric ages were obtained; the unit's condition (named or unnamed) is stated. We have also qualified nomenclatural status of named unit as formal or informal according to whether or not they meet the provisions of the North American Stratigraphic Code (NACSN, 2005) or of the pertinent code at the time of their proposal. All unnamed units are informal.

The third column provides the site coordinates to the nearest minute based on published information, or is inferred from information given in the referred article; this last mode is expressed by an ampersand (&) as a footnote designator.

Radiometric Aspect

The fourth column bears the numerical ages, expressed as kiloanni (ka). The fifth column lists the dated material and the method of dating used: K-Ar (sensu Bonhomme et al., 1975), ^{40}Ar - ^{39}Ar (sensu van der Pluijm et al., 2006), fission track (sensu Günther and Van den Haute, 1992), standard ^{14}C (sensu Libby, 1946; Anderson et al., 1947; Geyh and Schleicher, 1990), or accelerator mass spectrometer (AMS) ^{14}C (sensu Gillespie et al., 1984). Because AMS analysis is still quite expensive, it was performed only in a few significant sites; in most sites the standard ^{14}C method was used.

Paleontological–Geochronological Aspect

The sixth column lists the names of the fossil assemblages studied. These may be a local fauna (l.f., an assemblage collected from a single locality or spatially very close localities), or a single occurrence (s.o., vertebrate remain[s] that belong to a single individual/taxon). These assemblages are usually named after a geographic feature.

The seventh column states the biochronological age of each assemblage in terms of the North American Land Mammal Ages (NALMA) as presented in Woodburne (2004) or in Bell et al. (2004) for the Irvingtonian and Rancholabrean NALMAs.

The Wisconsinan Glacial Episode, originally the classical Fourth Glacial Stage of the Pleistocene Epoch in North America (Neuendorf et al., 2005), is at present the only numerically defined and widely used Pleistocene glacial episode and mammalian age. It corresponds to the ~40–10 ka interval, its lower boundary coinciding with the lower practical limit of ^{14}C dating, and its upper with the Pleistocene/

Table 1 Radiometrically dated Pleistocene lithostratigraphic units that bear vertebrates assemblages.

Morphotectonic Province (MP)	State Site [Ref.]	Formation	Site Coordinates	Radiometric Age (in ka)*	Method	Local Fauna (l.f.) or Single Occurrence (s.o.)	NALMA#	Epoch##
NORTHWESTERN PLAINS AND SIERRAS MP								
SONORA STATE								
1. Térapa	[1a]	Tonibabi basalt flow [Informal]	29°41'N-109°39'W&	0.44 ± 0.13 440 ± 130* [Maximal age]	⁴⁰ Ar- ³⁹ Ar [Whole rock]	Térapa l.f. **[Estimated age: 570 ka to ... **...310 ka]	Middle Irvingtonian [Irvingtonian II]	Middle Pleistocene
	[1a, 1b]	Unnamed Lower lava flow	29°39'N-109°28'W	0.3 ± 0.1 300 ± 100*	⁴⁰ Ar- ³⁹ Ar [Whole rock]		Late Irvingtonian [Irvingtonian III]-Early Rancholabrean** Rancholabrean**	Late Pleistocene
				1.7 ± 0.74 1,700 ± 740*	⁴⁰ Ar- ³⁹ Ar [Whole rock]			Early Pleistocene
				[Maximal age]	⁴⁰ Ar- ³⁹ Ar [Whole rock]			Middle Pleistocene
	[1a, 1b]	Unnamed Upper lava flow	29°41'N-109°28'W	0.61 ± 0.08 610 ± 80* [Maximal age]	⁴⁰ Ar- ³⁹ Ar [Whole rock]		Rancholabrean**	
			0.47 ± 0.006 470 ± 6* [Minimal age]	⁴⁰ Ar- ³⁹ Ar [Whole rock]				
SIERRA MADRE ORIENTAL MP								
NUEVO LEON STATE								
2. San Josecito Cave	[2]	Unnamed	24°06'N-99°49'W&	44.52*	¹⁴ C [Standard]	San Josecito l.f.	Late Rancholabrean	Late Pleistocene
	[2]			28.005*	¹⁴ C [Standard]		Wisconsinan	Late Pleistocene
	[3]	Unnamed	23°48'N-100°42'W&	33.3*	¹⁴ C [Standard]	El Cedral l.f.	Wisconsinan	Late Pleistocene
TRANS-MEXICAN VOLCANIC BELT MP								
MEXICO STATE								
4. Santa Isabel Ixtapan	[4]	Unnamed	19°34'N-98°56'W&	16.0*	¹⁴ C [Standard]	Santa Isabel Ixtapan l.f.	Wisconsinan	Latest Pleistocene
	[4]		19°34'N-98°56'W&	11.003*	¹⁴ C [Standard]	Santa Isabel Ixtapan l.f.	Wisconsinan	Latest Pleistocene
	[4a]		19°34'N-98°56'W&	14.500*	¹⁴ C [Standard]	Santa Isabel Ixtapan l.f.		
			19°34'N-98°56'W&	10.800*	¹⁴ C [Standard]	Santa Isabel Ixtapan l.f.		
5. Zohapilco [In Tlapacoya Municipio]	[4]	Unnnamed	19°19'N-98°54'W&	14.77	¹⁴ C [Standard]	Zohapilco l.f.	Wisconsinan	Latest Pleistocene
	[4]	Unnnamed	19°38'N-99°38'W&	11.58*	¹⁴ C [Standard]	Santa Lucía l.f.	Wisconsinan	Latest Pleistocene
7. Santa Lucía I	[4]	Unnnamed	19°38'N-99°38'W&	26.3*	¹⁴ C [Standard]		Wisconsinan	Late Pleistocene
	[4]		19°38'N-99°38'W&	23.9*	¹⁴ C [Standard]		Wisconsinan	Late Pleistocene
8. Santa Lucía II	[4]	Unnnamed	19°38'N-99°38'W&	11.17*	¹⁴ C [Standard]		Wisconsinan	Latest Pleistocene
	[4]	Unnnamed	19°17'N-98°53'W&	33.5*	¹⁴ C [Standard]	Tlapacoya l.f.	Wisconsinan	Late Pleistocene
9. Tlapacoya	[4]		19°17'N-98°53'W&	21.7*			Wisconsinan	Late Pleistocene
			98°53'W&					
10. Tlapacoya I	[5]	Unnnamed	19°17'N-98°53'W&	10.2 ± 0.065*	⁴ C [AMS]		Wisconsinan	Latest Pleistocene

Table 1 Continued.

Morphotectonic Province (MP)	State Site [Ref.]	Formation	Site Coordinates	Radiometric Age (in ka)*	Method	Local Fauna (l.f.) or Single Occurrence (s.o.)	NALMA#	Epoch#
11. Acambay	[6]	Unnamed	19°57'N-99°50'W&	1.2 ± 0.13 [Minimal age]	Fission Tracks [Zircon]	Acambay l.f.	Irvingtonian [Irvingtonian I] [Rancholabrean/Blancan]**	Early Pleistocene
12. Tepexpan	[7]	Unnamed	19°37'N-99°56'W&	19.11 ± 90* [Maximal age] 16.73 ± 75* [Maximal age]	¹⁴ C [AMS] ¹⁴ C [AMS]	Tepéxpan l.f. or s.o.	Wisconsinan	Late Pleistocene
13. San Miguel Tocuila	[8] [8a] [8b]	Unnamed	19°31'N-99°54'W	12.615 ± 75* 10.22 ± 75* 11.1 ± 0.08* 11.277 ± 139* 11.274 ± 116* 11.541 196* 11.296 ± 230-270* 10.553 ± 188* 11.225 ± 75*	¹⁴ C [AMS] ¹⁴ C [AMS] ¹⁴ C [AMS] ¹⁴ C Standard ¹⁴ C Standard ¹⁴ C Standard ¹⁴ C Standard ¹⁴ C Standard ¹⁴ C [AMS]	Tocuila s.o.	Wisconsinan	Late Pleistocene
DISTRITO FEDERAL = CIUDAD DE MEXICO								
14. San Bartolo Atepehuacan	[4]		19°29'N-99°08'W&	31.85*	¹⁴ C [Standard]	San Bartolo Atepehuacan l.f.	Wisconsinan	Late Pleistocene
15. Ciudad de los Deportes	[4]	Unnamed	19°24'N-99°05'W&	18.7*	¹⁴ C [Standard]	Ciudad de los Deportes l.f.	Wisconsinan	Latest Pleistocene
16. Peñon III	[6]	Unnamed	19°26'N-99°04'W&	10.755 ± 0.075*	¹⁴ C [AMS]		Wisconsinan	Latest Pleistocene
PUEBLA STATE								
17. Valsequillo	[4] [9]	Unnamed	18°54'N-98°06'W&	20.78* 38.9 ± 0.8* 36.95 ± 0.6* 30.62 ± 0.14* 27.88 ± 0.12* 25.08 ± 130*	¹⁴ C [Standard] ¹⁴ C [AMS]	Valsequillo l.f.	Wisconsinan	Late Pleistocene
SIERRA MADRE DEL SUR MP								
OAXACA STATE								
18. San Marcos Necoxtla	[4]	Unnamed	18°33'N-97°21'W&	14.96*	¹⁴ C [Standard]	San Marcos Necoxtla l.f.	Wisconsinan	Latest Pleistocene
19. Guilá Naquitz	[4]	Unnamed	16°57'N-96°22'W&	10.7*	¹⁴ C [Standard]	Guilá Naquitz l.f.	Wisconsinan	Latest Pleistocene
SIERRA MADRE DE CHIAPAS MP								
CHIAPAS STATE								
20. Punta de Llano	[10]	Punta de Llano [Formal]	16°48'N-92°52'W	0.56 ± 0.07 560 ± 70* [Minimal age]	K-Ar [Amphibole]	Arroyo Limas s.o.	Early Irvingtonian [Irvingtonian II]	Middle Pleistocene
	[10]		16°48'N-92°52'W	0.37 ± 0.26 370 ± 260* [Minimal age]	K-Ar [Plagioclase]		Late Irvingtonian [Irvingtonian III]	Late Pleistocene

Table 1 Continued.

Morphotectonic Province (MP)	State Site [Ref.]	Formation	Site Coordinates	Radiometric Age (in ka)*	Method	Local Fauna (l.f.) or Single Occurrence (s.o.)	NALMA#	Epoch#
21. Chiapa de Corzo	[11]	Unnamed	16°42'N-92°59'W&	0.45 ± 0.13 450 ± 130* [Minimal age]	K-Ar [Plagioclase]	Arroyo Nandalumí s.o.	Middle Irvingtonian [Irvingtonian II]	Middle Pleistocene
	[11]		16°42'N-92°59'W&	0.35 ± 0.19 350 ± 190* [Minimal age]	K-Ar [Plagioclase]		Late Irvingtonian [Irvingtonian III]	Late Pleistocene

Ref. = References [two kinds: **RCH**, radiometric references, and **BCH**, biochronologic references; both are indicated by a number in brackets besides the locality name].
*Asterisked numbers indicate ka (one kiloyear, 1000 years), numbers without asterisk indicate Ma (one mega-annum, one million years before the present).
** Double-asterisked NALMA is the age assigned by the original authors; it differs from the corresponding numerical age, see text for details.
#Geochronometric NALMA [North American Land Mammal Age] boundaries after Woodburne (2004), particularly Bell et al. (2004), Blancan-Rancholabrean, Pliocene-Pleistocene).
&#Geochronometric Stage/Age, and Epoch boundaries after Gradstein et al. (2004).
& Latitude-Longitude of RCH sampling site not stated by author; coordinates inferred from information presented in the referred article.
Ref. [1RCH]: 1a and 1b, Paz-Moreno et al. (2003). **[1BCH]:** 1a, Mead et al. (2006, 2007); 1b, Carranza-Castañeda and Roldán-Quintana (2007). **[2RCH]:** Arroyo-Cabral et al. (1995). **[2BCH]:** Ferrusquía-Villafranca et al. (2010 and lit. therein). **[3RCH]:** Lorenzo and Mirambell (1986a). **[3BCH]:** Ferrusquía-Villafranca et al. (2010 and lit. therein). **[4RCH]:** Arroyo-Cabral et al. (2002). **[4aRCH]:** González et al., 2015. **[4BCH]:** Arroyo-Cabral et al., 2002, 2005. **[5RCH]:** González et al. (2003). **[5BCH]:** Ferrusquía-Villafranca (2010). **[6RCH]:** Mercer et al. (2003), Mercer (2004). **[6BCH]:** Israde-Alcántara et al. (2010). **[7RCH]:** Lamb et al. (2009). **[7BCH]:** Lorenzo and Mirambell (1986b). **[8RCH]:** Siebe et al. (1999); **[8aRCH]:** Arroyo-Cabral et al., 2002, 2005. **[8bRCH]:** Moret et al. (2003). **[8cRCH]:** González et al., 2014. **[9RCH]:** González et al. (2006). **[9BCH]:** Ferrusquía-Villafranca et al. (2010). **[10RCH]:** Ferrusquía-Villafranca (1996). **[10BCH]:** Ferrusquía-Villafranca et al. (2010). **[11RCH]:** Ferrusquía-Villafranca and McDowell (1991). **[11BCH]:** Ferrusquía-Villafranca et al. (2010).

Holocene boundary, commonly set at 10 ka to 11.5 ka (Bell et al., 2004; Gradstein et al., 2004). The Calibrated Polarity Geochron Timetable was not used for this project because the Brunhes (normal) Chron starts at 780 ka, (Gradstein et al., 2004), and thus spans the Wisconsinan Glacial Episode as well as the Middle and Late Pleistocene.

The eighth column lists the geochronological information expressed in epochs and periods sensu Gradstein et al. (2004).

Footnotes

The footnotes provide the radiometric geochronological and biochronological references used here, which are keyed to the bracketed number on the right of the first column. Some papers refer to two or more sites. When sites have been independently studied by two different research teams, we have cited both; and in the “Discussion” section we provide our parsimonious assessment of such data.

The acronym QMMDB (Quaternary Mexican Mammals Data Base) refers to the so-named database housed and maintained in the Laboratorio de Arqueozoología Ticúl Alvarez Solórzano, Subdirección de Investigación, INAH, Moneda 16, Centro Histórico, Ciudad de México. This database includes geographical, paleontological, and, in some instances, radiometric information. It was used as data source for some sites/faunas. Arroyo-Cabral et al. (2002) described the QMMDB and made it known to the interested community.

Terminology

The sedimentary petrographic nomenclature follows Folk (1974) and Boggs (1995), the pyroclastic terminology used is that of Fisher and Schmincke (1984), and the sedimentary facies nomenclature follows Miall (2006, 2010) for the fluvial facies and Collinson (1996) for the lacustrine facies. In some instances, old descriptions were redescribed or interpreted using current terminology and/or conceptions. The mammalian systematics is that of McKenna and Bell (1997). Finally, it should be noted that the acronyms used are defined the first time they appear in the text.

RESULTS AND DISCUSSION

Table 1 provides a summary of the geographical, geologic, and geochronological information for sites/localities where both radiometrically dated lithostratigraphic units and studied vertebrate fossils co-occur. These are treated in geochronological order. For each site, the geologic setting is presented and discussed first; then its radiometric dating and vertebrate fossil assemblage is treated and discussed, together with the regional significance of both the geologic and paleontological data.

INTRODUCTORY REMARKS

México’s continental Pleistocene is stratigraphically undifferentiated for the most part. Detailed geologic information for the 21 sites considered is largely nonexistent and formal lithostratigraphic units are the exception. Hence, the summary presented below largely draws from regional sources: Mooser (1975); Servicio Geológico Mexicano (SGM 1992, 1996a, 1996b); Instituto Nacional de Estadística, Geografía e Informática (INEGI 1982a, 1982b, 1983); some local sources, for example, Schlaepfer (1968); INEGI (1971, 1974, 1979a, 1979b); Mooser et al. (1996), Mercer (2004), Mead et al. (2006), Carranza-Castañeda and Roldan-Quintana (2007), and firsthand knowledge of some sites.

Fourteen out of the 21 sites lie in the Trans-Mexican Volcanic Belt morphometric province (TMVB MP), two in the Sierra Madre Oriental MP (SMOr), two in the Sierra Madre de Chiapas MP (SMOr hereafter), and two each in the Northwestern Plains and Sierras MP (NW hereafter) and the Sierra Madre del Sur MP (SMS hereafter); see

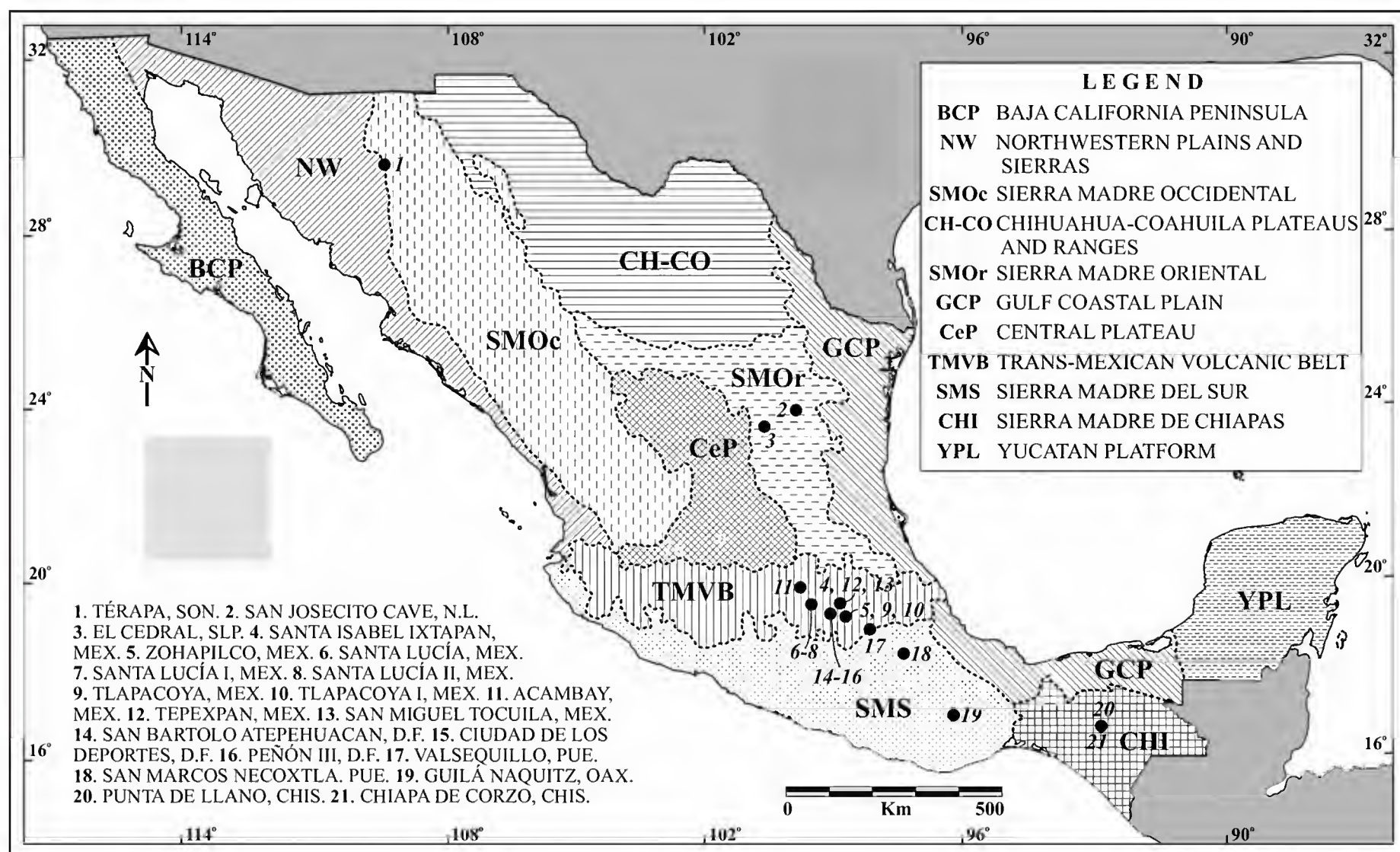


Figure 1 Morphotectonic provinces map of México showing the location of Pleistocene sites with radiometrically dated lithostratigraphic units that bear studied vertebrates.

Figure 1. The sites from the Basin of México will be treated elsewhere (see “Latest Pleistocene” section).

The sedimentary sequence in most sites is a few dozens of meters thick and horizontal-lying, so that it unconformably overlies the usually tilted Tertiary units, and it commonly includes both fluvial and lacustrine deposits. The fluvial ones largely consist of fine to coarse-grained, cross-bedded, friable to moderately indurated volcanenitic sandstone, siltstone, and claystone set in thin to medium strata (channel and overbank facies); smaller amounts of clast-supported, pebble to cobble conglomerate of volcanic clasts set in medium to thick strata (largely channel facies). In addition, the sequence includes parallel-bedded, friable to moderately indurated, fine-grained clayey siltstone, claystone –silty at times—set in laminar to thin strata (clastic lacustrine facies); frequently the lake facies bear diatoms, ostracods, palynomorphs, and other microfossils. Thin sheets of felsic ash–fall tuff (pyroclastic facies) are sparsely interbedded in the sequence (fluvial, lacustrine, or mixed) at various stratigraphic levels.

In the sites where both fluvial and lacustrine deposits are present, they exhibit a variety of space-stratigraphic relationships as follows: (a) one lies above the other through gradual or, less commonly, abrupt contacts; (b) they alternate in a rhythmic to pattern-less fashion and the lacustrine and fluvial stratal packages may be of different thickness (or less commonly of similar thickness); (c) they intertongue, forming sequences of complex sedimentary architecture; and/or (d) a combination of two or more space relationships.

The fossil vertebrates commonly occur in the fine-grained fluvial facies; however, not infrequently, the lacustrine facies has also yielded such fossils. The terrestrial vertebrate fossils belong to communities living on the lowlands/valleys commonly associated with fluvial courses, ponds, or lakes, and/or on the slopes of the mountainous countryside. Aquatic

vertebrates like turtles, crocodiles, and fish are well represented in fluvial and lacustrine deposits; a few mammals (e.g., hydrochoerids) are also represented in this kind of deposits. Along the Trans-Mexican Volcanic Belt, numerous lakes were formed, probably not simultaneously but within a short time span (Ferrari et al., 2012); some are still present, for example, Chapala, Jalisco; Cuitzeo, Michoacán; Texcoco, México.

Two sites have a different geologic setting: Site 2, San Josecito Cave, Nuevo León, is formed by “cave deposits” (largely fine-grained clastic debris fills, underground pond/fluvial deposits, and, less commonly, speleothems). Site 13, San Miguel Tocuila, Estado de México, is a ~1.3-m-thick lahar (i.e., a volcanic mud flow deposit) bearing the remains of at least seven mammoths, as well as scattered bones and fragments (González et al., 2001:705); both will be discussed in the Part 3-Other Wisconsinan Sites.

The main geologic contribution derived from the Pleistocene sites and their mammal faunas is threefold:

1. They document the far more humid environment prevailing during this epoch in México.
2. They document greater mammalian biodiversity during this time.
3. They document dramatic environmental changes that took place at the Pleistocene’s end, which drastically modified both the landscape and the mammal assemblages in México by the Early Holocene (see Ferrusquía-Villafranca et al., 2010 for a general review of this subject).

LATE EARLY–MIDDLE PLEISTOCENE

Acambay Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 11)

Table 2 Acambay local fauna, Irvingtonian, México State, TMVB MP.

CLASS MAMMALIA
ORDER PERISSODACTYLA
Equidae
<i>Equus simplicidens</i>
ORDER ARTIODACTYLA
Camelidae
<i>Genus and species indet.</i>
ORDER PROBOSCIDEA
Gomphotheriidae
<i>Rhynchotherium</i> sp.

Source: Israde-Alcántara et al. (2010).

GEOLOGIC SETTING. The vertebrate-bearing sequence according to Israde-Alcántara et al. (2010) is ~70 m thick and includes three units. The lowest unit is ~50 m thick, consists of diatomite, fine-grained volcanoclastics, and claystone intruded by sand dikes. The middle unit unconformably overlies the lower one, is 2–22 m thick, and comprises diatomite and siltstone that grades upward into a thick bed set of laminated diatomite, covered by a 0.01-m-thick, felsic-ash fall sheet, in turn covered by a ~2-m-thick layer of slump-structured diatomite. The uppermost unit (of unstated thickness) is capped by siltstone and sandstone beds that show liquefaction structures. The mammals reported from them by Israde-Alcántara et al. (2010:82) were collected from undescribed "...upper units beneath this ash." These authors also mention that undescribed Pleistocene mammals have been collected earlier in this site by local people, but their precise provenance is unknown; they include horse, camel, bison, and mammoth.

RADIOMETRIC/BIOCHRONOLOGICAL DATING AND REGIONAL SIGNIFICANCE. The tuff sheet overlying the mammal-bearing strata yielded a fission track age of 120 ± 0.13 ka (Table 1; Mercer et al., 2003; Mercer, 2004), which places it in the late Early Pleistocene (Gradstein et al., 2004). The mammals collected below the tuff sheet (depth/distance not stated), here designated Acambay local fauna (Table 2), comprise perissodactyls (Equidae), artiodactyls (Camelidae), and proboscideans (Gomphotheriidae; Israde-Alcántara et al., 2010). Largely on the basis of the equid *Equus simplicidens*, this fauna is assigned to the Blancan (Israde-Alcántara et al., 2010:87); however, the evidence is not compelling: As late as 1987 (Lundelius et al., 1987), the Blancan was not formally defined (sensu Woodburne, 1977), but characterized by several taxa including *Equus (Dolichohippus) simplicidens* (Bell et al., 2004:249), which is no longer regarded as a Blancan index in the current definition and characterization of this NALMA (Bell et al., 2004:250). The Blancan/Irvingtonian boundary is diachronous, being set at 1.9–1.7 Ma (Bell et al., 2004) but older than the 1.2 ± 0.13 -Ma age yielded by the overlying tuff. On these grounds, we assigned the Acambay l.f. to the Irvingtonian NALMA (probably Irvingtonian I). The stratigraphic uncertainty regarding the provenance of other unstudied mammals collected by local people precludes assigning them a more precise age beyond Pleistocene.

Punta de Llano Site (Chiapas State, Sierra Madre del Sur MP, Fig. 1, Site 20)

Chiapa de Corzo Site (Chiapas State, Sierra Madre del Sur MP, Fig. 1, Site 21)

GEOLOGIC SETTING. The sequence from the Punta de Llano site belongs to the Punta de Llano Formation (Ferrusquía-Villafranca, 1996), a 20–30-m-thick unit largely consisting of fine-grained, tabular cross-bedded, volcanoclastic sandstone and siltstone set in thin to medium strata (fluvial, mainly channel facies), and lesser amounts of friable silty claystone set in thin strata (fluvial, overbank facies), as well as a clast-

supported, pebble, polymictic, cross-bedded litharenitic conglomerate set in medium to thick strata (fluvial, channel facies); additionally, thin sheets of felsic, largely ash-fall and ash-flow tuff, sparsely interbedded and/or cover the epiclastic strata (pyroclastic facies). The unnamed sequence from the Chiapa de Corzo site is thinner (~12–15 m thick), but otherwise similar to that of the Punta de Llano site.

RADIOMETRIC/BIOCHRONOLOGICAL DATING AND REGIONAL SIGNIFICANCE. The tuff sheets overlying mammal-bearing strata at both sites yielded ages as follows: Punta de Llano site, 560 ± 0.007 ka (K-Ar) and 370 ± 260 ka (K-Ar); and Chiapa de Corzo site, 450 ± 130 ka (K-Ar) and 350 ± 190 ka (K-Ar, Table 1; Ferrusquía-Villafranca, 1996; Ferrusquía-Villafranca et al., 2010). These dates place the sequence of both sites in the Middle Pleistocene (Gradstein et al., 2004).

The only mammal taxon recovered from these sites is the long-lived proboscidean gomphotheriid *Cuvieronius* sp. (Miocene to Pleistocene; McKenna and Bell, 1997); here the radiometric dating allows us to assign it to the Middle Pleistocene, that is, Irvingtonian, probably the Irvingtonian II NALMA (Bell et al., 2004). Irvingtonian faunas in México are little known, in fact the Sonoran El Golfo fauna (Shaw, 1981; Shaw and McDonald, 1987), is the only one reported; therefore, the *Cuvieronius* finds from Chiapas significantly add to this meager record.

LATE PLEISTOCENE

Térapa Site (Sonora State, Northwestern Plains and Sierras MP, Fig. 1, Site 1)

GEOLOGIC SETTING. The site lies in the Quaternary Moctezuma Volcanic Field (QMVf herein) in northeastern western Sonora (Paz-Moreno et al., 2003). The fossiliferous sequence occupies a small basin (2 km²), seemingly formed by a basalt flow diversion of the river course in the upper Río Moctezuma valley (Mead et al., 2006). The basin is delimited on the north, west, and south by tholeiitic basalt flows, informally designated by Mead et al. (2006) as the Tonibabi Basalt Flow. In this basin, a fine-grained clastic sequence was deposited. It is ~11 m thick as reported by Mead et al. (2006) or 20 m thick according to Carranza-Castañeda and Roldán-Quitana (2007). Seemingly unaware of the work by Mead et al. (2006), Carranza-Castañeda and Roldán-Quitana (2007) studied the same site and reported a small mammal assemblage. The sequence description that follows draws from both sources.

The sequence largely consists of parallel-bedded, friable to moderately indurated, richly fossiliferous silty claystone set in thin strata (lake or probably marsh facies) and lesser amounts of medium- to fine-grained, tabular cross-bedded volcanoclastic sandstone and siltstone set in thin to medium strata, as well as a few strata of clast-supported conglomerate (fluvial facies). Friable sandstone and conglomerate strata unconformably overlie the sequence.

According to Mead et al. (2006:229), this sequence overlies and abuts the Tonibabi Basalt Flow, which, in the nearby La Carbonera Canyon, yielded a ⁴⁰Ar-³⁹Ar age of 440 ± 130 ka, thus placing the flow in the Middle Pleistocene (Gradstein et al., 2004). They also stated that the relationship between this flow and those basalt flows studied by Paz-Moreno et al. (2003) is not well understood. On the other hand, Paz-Moreno et al. (2003), who studied the QMVf, mentioned that the fissure-erupted tholeiitic basalt flows that form the best part of this field yielded a ⁴⁰Ar-³⁹Ar age of 1700 ± 740 ka (Paz-Moreno et al., 2003:table 1; Ma converted to ka), and also reported that monogenetic cone-erupted alkaline basalt flows geochemically related to the tholeiitic ones, have yielded a K-Ar age of 530 ± 200 ka (Paz-Moreno et al.,

2003:443), as well as ^{40}Ar - ^{39}Ar ages of 610 ± 80 ka, 470 ± 60 ka, and 300 ± 11 ka (Paz-Moreno et al., 2003:table 1; Ma converted to ka), concluding that the latter volcanism was younger than the tholeiitic one. However, in their abstract, they stated that the youngest such flows have an age of 530 ka, thus omitting younger-aged flows.

Radiometric datum reported by Mead et al. (2006), and those from the monogenetic cone-erupted flows (Paz-Moreno et al., 2003:table 1), led them to postulate that the sedimentary sequence was laid down at some time between 510 and 310 ka. On the other hand, Carranza-Castañeda and Roldán-Quintana (2007:84), mention that the sequence overlies olivine basalt flows of ages between 170 ± 074 ka and 610 ± 80 ka (quoting as source Paz-Moreno et al., 2003), which places the flows in the Early–Middle Pleistocene (Gradstein et al., 2004). However, in their figure 4, Carranza-Castañeda and Roldán-Quintana, (2007:84), label the basalt flows as >1700 ka. Thus, the stratigraphic interpretations of Mead et al. (2006) and Carranza-Castañeda and Roldán-Quintana (2007) are clearly different, but do not furnish enough information to select one over the other. We have left them as alternative interpretations. Clearly, additional work is needed to assess these different interpretations.

RADIOMETRIC/BIOCHRONOLOGICAL DATING AND REGIONAL SIGNIFICANCE. Radiometric dating has already been discussed. The Térapa local fauna (Table 3), a name coined by Mead et al. (2006), contains crocodiles and the following mammal taxa (Mead et al. 2006, 2007; Carranza-Castañeda and Roldán-Quintana, 2007): xenarthrans (Pampatheriidae and Glyptodontidae), carnivorans (Canidae, Felidae, and Procyonidae), rodents (Geomyidae, Hydrochoeridae, and Muridae), lagomorphs (Leporidae), perissodactyls (Equidae and Tapiridae), artiodactyls (Antilocapridae, Bovidae, Camelidae, Cervidae, and Tayassuidae), and proboscideans (Elephantidae and Gomphotheriidae). Largely based on the presence of *Bison*, a Pleistocene index taxon (Bell et al., 2004), as well as of *Equus conversidens* and *E. excelsus*, both Mead et al. (2006) and Carranza-Castañeda and Roldán-Quintana (2007) assigned the Térapa l.f. to the Rancholabrean NALMA (Bell et al., 2004), but that of the latter seems to be older. However, the beginning of the Rancholabrean NALMA is usually placed at 0.12 Ma (Bell et al., 2004), being largely identified by the presence of *Bison*, a datum ~ 200 ka later than the postulated deposition time of the vertebrate-bearing sequence proposed by Mead et al. (2006). Attempting to solve this timing incongruity, they claimed that earlier records of *Bison* are known, for example, those from the Ten Miles Hill beds, North and South Carolina, between 240 and 200 ka (Sanders, 2002), and from other records (see Sanders, et al., 2009) published later than Mead et al. (2006), so that the Térapa *Bison* might be one such early record. Again, further work is needed to clarify this issue.

Additionally, it should be noted that the presence of aquatic vertebrates (e.g., crocodiles, tapirs, and hydrochoerids) in the Térapa l.f., which at present live in tropical regions hundreds of kilometers (even thousands in the case of hydrochoerids) south of northwestern Sonora, where very arid conditions prevail today, evidences the profound environmental change that must have occurred in Sonora since the Late Pleistocene/Early Holocene. In this regard alone, this fauna is quite significant.

LATEST PLEISTOCENE

San Josecito Cave Site (Nuevo León State, Sierra Madre Oriental MP, Fig. 1, Site 2)

Tlapacoya Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 9)

Tepexpan Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 12)

San Bartolo Atepehuacan Site (Distrito Federal State, now Ciudad de México, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 14)

Valsequillo Site (Puebla State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 17)

El Cedral Site (San Luis Potosí State, Sierra Madre Oriental MP, Fig. 1, Site 3)

Santa Isabel Ixtapan Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 4)

Zohapilco Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 5)

Santa Lucía Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 6)

Santa Lucía I Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 7)

Santa Lucía II Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 8)

Tlapacoya I Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 10)

San Miguel Tocuila Site (México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 13)

Ciudad de los Deportes Site (Distrito Federal State, now Ciudad de México, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 15)

Peñón III Site (Distrito Federal, now Ciudad de México State, Trans-Mexican Volcanic Belt MP, Fig. 1, Site 16)

San Marcos Necoxtla Site (Puebla State, Sierra Madre del Sur MP, Fig. 1, Site 18)

Guilá Naquitz Site (Oaxaca State, Sierra Madre del Sur MP, Fig. 1, Site 19)

PART 1—GENERAL ASPECTS

Geologic Setting. Excluding the sites already discussed, that is, Site 1, Térapa; Site 11, Acambay; Site 20, Punta de Llano; and Site 21 Chiapa de Corzo, the remaining 17 sites listed in Table 1 have yielded Wisconsinan faunas (see below), and could be regarded as local samples of a single chronofauna; on this basis, they are discussed together.

Geochronological Framework. The Middle/Late Pleistocene boundary is set at 0.126 Ma and that of the Late Pleistocene/Holocene at 0.0115 Ma (Gradstein et al., 2004). The Late Pleistocene interval includes the Rancholabrean NALMA, which spans the ~ 0.120 – 0.010 -Ma interval (Bell et al., 2004). It should be noted that the numerical divisions of the NALMAs (Woodburne, 2004) have been established using the geochronometric dates afforded by the radiometrically calibrated Geomagnetic Polarity Time Table (or Time Scale). However, this is not possible for the Rancholabrean NALMA, because the Brunhes (normal) Polarity Chron spans the Rancholabrean–Holocene time interval (Gradstein et al., 2004), thus precluding numerical subdivision in smaller time units or “subages”; the Wisconsinan SubNALMA is the only exception.

This term originally referred to the Fourth Glacial Stage of the Pleistocene Epoch in North America (Neundorff et al., 2005), but currently it corresponds to the chrono-interval whose starting time is determined by the maximal practical limit/time-resolution of the ^{14}C dating methods (i.e., ~ 40 ka), and its termination by the Pleistocene/Holocene time boundary, usually set at 10 to 11.5 ka (Bell et al., 2004; Gradstein et al., 2004). The Wisconsinan is widely used in Quaternary studies and here we use it for the youngest portion of the Rancholabrean NALMA.

Chronological Spread of the Sites. The 17 Wisconsinan mammal faunas listed in Table 1 show the following time spread: only San Josecito Cave (Site 2) has an age >40 ka; three faunas, Tlapacoya (Site 9), San Bartolo Atepehuacan (Site 14), and El Cedral (Site 3) have ages between 40–30 ka; two, Valsequillo (Site 17) and Santa Lucía I (Site 7)

Table 3 Térapa mammal local fauna, Early Rancholabrean, Sonora, Northwestern Plains and Sierras MP.

XENARTHRA
Dasypodidae
<i>Pampatherium mexicanum</i> †
Glyptodontidae †
<i>Glyptotherium cylindricum</i> †
CARNIVORA
Canidae
<i>Canis dirus</i> †
Felidae
<i>Lynx rufus</i>
Procyonidae
<i>Procyon lotor</i>
RODENTIA
Geomyidae
<i>Geomys</i> sp.
Hydrochoeridae
<i>Hydrochoerus</i> sp.
Muridae
<i>Neotoma</i> sp.
<i>Sigmodon</i> sp.
LAGOMORPHA
Leporidae
<i>Sylvilagus</i> sp.
PERISSODACTYLA
Equidae
<i>Equus</i> sp.
Tapiridae
<i>Tapirus</i> sp.
ARTIODACTYLA
Antilocapridae
<i>Capromeryx</i> sp.
<i>Stockoceros</i> sp.
Bovidae
<i>Bison</i> sp. †
Camelidae
<i>Camelops</i> sp. †
Cervidae
<i>Odocoileus</i> sp. †
Tayassuidae
<i>Platygonus</i> sp. †
PROBOSCIDEA
Elephantidae
<i>Mammuthus</i> sp. †
Gomphotheriidae †
<i>Cuvieronius</i> sp. †

† Extinct taxon.
Source: Mead et al. (2006, 2007) and Carranza-Castañeda and Roldán Quintana (2007).

have ages between 30-20 ka; another two, Tepexpan (Site 12) and Ciudad de los Deportes (Site 15) have ages between 20-15 ka; the remaining nine faunas, Santa Isabel Ixtapan (Site 4), Zohapilco (Site 5), Santa Lucía (Site 6), Tlapacoya I (Site 10), San Miguel Tocuila (Site 13), Peñón III (Site 16), San Marcos Necoxtla (Site 18), and Guilá Níquitz (Site 19) have ages between 15-10 ka. Methodologically, three faunas, Tepexpan (Site 12), Peñón III (Site 16), and Tlapacoya I (Site 10) have only been dated by AMS ¹⁴C techniques; 12 faunas have been dated by standard ¹⁴C techniques; and two, San Miguel Tocuila (Site 13) and Valsequillo (Site 17) have been dated using both techniques. It should be noted that, except for San Miguel Tocuila (Site 13), the more expensive AMS ¹⁴C technique has only been applied in those faunas where human fossils or artifacts have been recorded.

Geographical Distribution of the Sites. The Wisconsinan sites/ faunas (Fig. 1) show the following space distribution: San Marcos Necoxtla, Puebla (Site 18), and Guilá Naquit, Oaxaca (Site 19), lie in the Sierra Madre del Sur MP; San Josecito Cave, Nuevo León (Site 2),

and El Cedral, San Luis Potosí (Site 3) lie in the Sierra Madre Oriental MP; the other 13 lie in the Trans-Mexican Volcanic Belt MP (one in Puebla: Valsequillo Site 17); three in the Distrito Federal, now Ciudad de México: San Bartolo Atepehuacan (Site 14), Ciudad de los Deportes (Site 15), and Peñón III (Site 16); the remaining nine lie in the State of México: Santa Isabel Ixtapan (Site 4), Zohapilco (Site 15), Santa Lucía (Site 6), Santa Lucía I (Site 7), Santa Lucía II (Site 8), Tlapacoya (Site 9), Tlapacoya 1 (Site 10), Tepexpan (Site 12), and San Miguel Tocuila (Site 13).

PART 2—BASIN OF MÉXICO SITES

Geologic Setting. Out of the 17 Wisconsinan mammal-bearing sites, 15 are set in fluvial/lacustrine sequences, and most lie in the Basin of México, in the eastern part of the Trans-Mexican Volcanic Belt MP (Fig. 2); therefore it is necessary to review/discuss its geology. This basin has been the subject of numerous studies, including geological and (Bryan, 1948; Arellano, 1951/1953; Zeevaert, 1953, Mooser 1961, 1975; Schlaepfer, 1968; Vázquez-Sánchez and Jaimes-Palomera, 1989; Enciso de la Vega, 1992) geological/geophysical studies (de Cserna et al., 1987) as well as those examining vertebrate paleontology (Hibbard, 1955), palynology (Sears and Clisby, 1955), limnology/environmental factors (Bradbury, 1971, 1989; Lozano-García and Ortega-Guerrero, 1997; Caballero-Miranda and Ortega-Guerrero, 1998; Caballero-Miranda et al., 1999), and paleosols (Bryan, 1948; Cabadas-Baez, 2007). Even so, its stratigraphy is far from being fully understood, largely because lack of detailed coordinated surface and subsurface studies. Nonetheless, integrating parsimoniously the relevant available multidisciplinary information (see Pleistocene Introductory Remarks above for other sources), it is possible to establish a highly plausible physical scenario for the Basin of México during the Wisconsinan.

Basin of México’s Theoretically Plausible Geographic/Geologic Wisconsinan Scenario. Basin Topographic Setting. The Basin of México lies in a high-altitude plateau surrounded by rugged country, which roughly defines a trapezoid-like outline (longer than wide), set NE–SW, it is ~115 km long (NE–SW) and ~68 km wide (minimal width, normal to basin length at middle part), and has an areal extent of ~9,600 km² (Fig. 2). Politically, the basin (Fig. 2) is part of the states of Hidalgo, Puebla (a very small part), Tlaxcala, México, and Distrito Federal and the cities of México and Pachuca; numerous towns and villages are located here.

Basin Boundaries and Interior Ranges. The basin, then as now, was largely surrounded by the Sierras de Pachuca, Chichicuatla, and Tepozán (in the northeast); Sierras de Calpulalpan, de Río Frío, and Nevada (in the southeast); Sierras del Chichinautzin (chiefly developed during the Early–Middle Wisconsinan), de las Cruces, de Monte Alto, and de Monte Bajo (in the south and southwest); and Sierras de Tezontlalpan, Tolcayuca, and Tepotzotlán (in the northwest). In general, such ranges stand ~200–1,000 m above the local basin floor, and even more so in the major volcanoes, being higher in the south and southeast (Fig. 2).

Smaller ranges within the basin, such as the Sierras de los Pinos, de Patlachique, de Guadalupe, and de Santa Catarina, stand ~200–400 m above the local basin level (Fig. 2). Some isolated mountains—Cerros Gordo, de Chiconautla, and del Peñón—stand ~120–300 m above its floor level. Both sierras and mountains were formed by Late Cenozoic volcanic successions, largely of intermediate to mafic composition. The rhyolitic to rhyodacitic component is less abundant. Geochronologically, those of the northeast are somewhat older.

Basin Floor. Regionally, the basin floor consists of a large plain gently dipping southward, and can be divided in three subregions: *Pachuca* (in the north), *Apan-Tecocomulco-Tochac* (in the northeast), and *Anahuac*, making up the southern part (see Fig. 2). *The first subregion* is the smallest, and stands between 2400 meters above sea level (masl) near

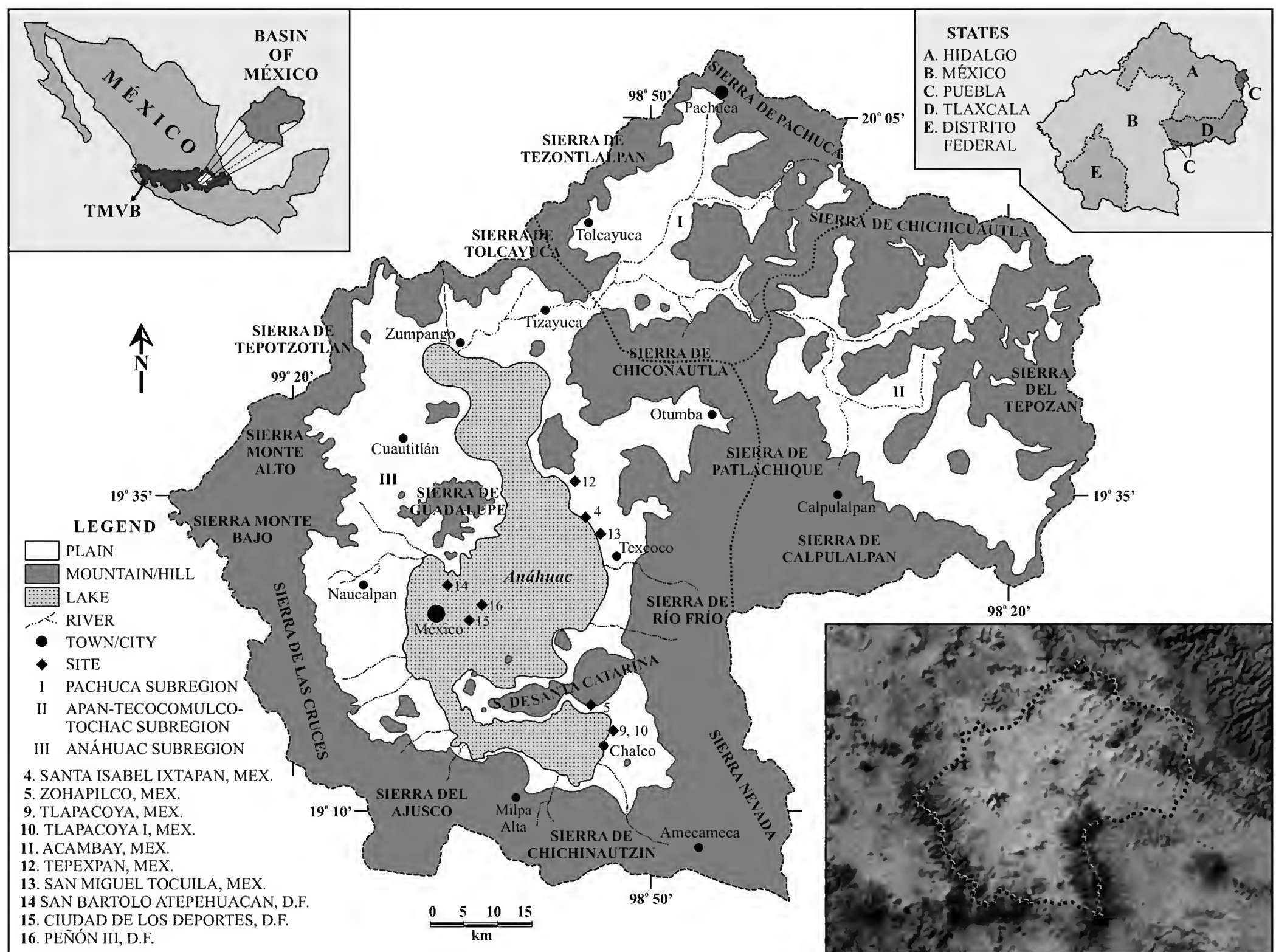


Figure 2 Map showing the Basin of México's generalized topographic setting inferred for Wisconsin time.

Pachuca and 2315 masl by the Sierras de Tezontlalpan, Tolcayuca, Chiconautla, and Pachuca. The *second subregion* includes the Apan, Tecocomulco, and Tochac valleys, which bear in their lowest parts the namesake remnant lakes. Such valleys stand at a different elevation: Tecocomulco (in the “local” west) at 2554 masl, Tochac (in the “local” east) at 2505 masl, and Apan (in the local center) at 2455 masl. The *third subregion*, Anahuac, is the largest, and stands at 2240 masl; México City lies here. It is bounded by the Sierras de Tolcayuca, Tepotzotlán, Monte Alto, Monte Bajo, de las Cruces, del Ajusco, Chichinautzin, Nevada, Río Frío, Patlachique, and Chiconautla. Within this subregion lie the Sierras de Guadalupe and Santa Catarina, as well as the Lakes Zumpango, Texcoco, Chalco, and Xochimilco.

Basin Drainage. The basin plain is traversed by an axial drainage (Fig. 2) that used to discharge in the south until blocked by the Sierra de Chichinautzin volcanic emplacement bracketed between 0.3959 and 0.014 Ma (Bloomfield, 1975; Martín del Pozzo, 1989; Siebe et al. 2004, 2005). This major event probably took place during the ~0.04–0.01 Ma interval (Velasco-Tapia and Verma, 2001).

The “axial channel” was arc-like, N–S trending, and set toward the west (it probably included the Río de las Avenidas). The largely E–W trending, longest tributary was set toward the north, barely connecting

the Pachuca and Apan-Tecocomulco-Tochac subregions. The main channels received water currents from the sierras’ foothills, for example, Ríos Tepotzotlán, Tlalnepantla, de los Remedios, San Juan de Dios (on the west), San José, and Amecameca (in the southwest). As mentioned above, in the subregions’ lowlands, lakes developed. In the Anahuac subregion, the now-separated Zumpango, Xaltocan, Texcoco, Xochimilco, and Chalco remnant lakes formed, in the recent past, the *Lago de Anahuac* (over 70 km long and ~40 km wide). The drainage blockage driven by the Chichinautzin event (Early–Middle Wisconsinan) probably played a significant role in its genesis.

Basin Sedimentary Processes. The fluvial network laid down alluvial fans in the foothills and basin floor interphase and surroundings, channel deposits along the stream floor, and overbank deposits, mainly floodplain facies, located in the river’s medium to distal parts; such facies frequently/intermittently became subaerially exposed, developing soils and a vegetation cover. Where the streams reached lakes, fluvial and lake deposits of complex sedimentary architecture were formed. The lake deposition was chiefly clastic, that is, clay, silt, and fine-grained sand; chemical deposition, mainly freshwater lime, was much less common. The lake shores and surrounding areas were partly marshy.

Volcanic Activity. Regional volcanic activity chiefly occurred in the surrounding sierras, producing ash-fall and ash-flow tuffs and lapilli tuffs that partly or fully covered the basin floor, forming thin pyroclastic/tephra sheets that became incorporated into the sedimentary lacustrine and fluvial sequences. It should be noted that three tephra layers have been extensively used as marker horizons within local lithostratigraphic site sequences, for example, Peñón Woman III, Tlapacoya, Metro Man, Chimalhuacan Man, and Tocuila (González et al., 2014, 2015). These are the Great Basalt Ash (GBA; *volcanic source*, Santa Catarina; *date*, $28,600 \pm 200$ years BP; Mooser, 1997; but see Ortega-Guerrero et al., 2015, who claim that the source is the monogenetic Teuhtli Volcano), Upper Toluca Pumice (UTP; *volcanic source*, Nevado de Toluca; *date*, $10,500 \pm 50$ years BP; Arce et al., 2003), and Pumice with Andesite tephra (PWA; *volcanic source*, Popocatepetl, *date*, 14,600 years BP; Mooser, 1967); it coincides with the Tutti Frutti Plinian fall deposit (see Siebe and Macías, 2004). Mafic lava flows, erupted from monogenetic volcanoes or through fissures, were also emplaced within the basin. The lava eruptions were less frequent than the pyroclastic ones.

Basin Sedimentation Controls and Paleocommunities. Both rivers and lakes responded to the short-term and/or long-term climatic events (including glaciations) and tectonic controls, thus generating a complex sedimentary/stratigraphic record that as yet is not well understood. The basin was home to large terrestrial and limnic communities that left an extensive record embedded in the basin's complexly structured sequence, which is only incompletely known.

Theoretically Plausible Geographical/Geologic Wisconsinan Scenario and the Currently Known Basin of México's Lithostratigraphy. The theoretically plausible Wisconsinan geographic/geologic scenario involves the known geomorphic features, that is, confining sierras/ranges, inner ranges and hills, basin shape, basin floor slope, basin drainage (axial channel, major tributary channels), and lakes. In this scenario, the geomorphic features are portrayed in a dynamic fashion:

1. Ranges and high lands are portrayed as source of pyroclastic and/or epiclastic sediments (from blocks to clay particles).
2. The fluvial network are portrayed as an efficient transporter of clastic sediments, as well as a multifaceted depositional agent that generates particular deposits at different sedimentary settings: (a) alluvial fans and talus deposits near the foothills, (b) channel deposits along the main current channels, (c) overbank deposits—chiefly floodplain fines, frequently subaerially exposed—in the medial and distal parts of a given stream, and (d) deposits of very complex sedimentary architecture at fluvial/lake interphases.
3. Lakes are portrayed as depo-centers largely of fine-grained clastic sediments. Freshwater limestone and other chemical precipitates are rather rare: for example, the travertine platform surrounding the Cerro del Peñón, generated by hot springs (González et al., 2015).
4. Frequent coeval volcanic activity is expressed as pyroclastic eruptions that generate thin tuff/tephra sheets that partly or fully covered the basin floor and/or surrounding slopes of hills and/or mountains, whereby piedmonts of complex makeup and architecture involving lake, fluvial, and pyroclastic/tephra facies are formed. This way, a dynamic linkage between the volcanic mountains, lakes, and fluvial network is established. Another expression of volcanic activity is the local emplacements of mafic lava flows related to monogenetic volcanoes (see Mooser, 1961, 1975).

The tangible record of such processes and events largely consists of depositional systems and volcanic rock bodies. The first include sedimentary sequences of particular attributes regarding general shape and configuration, grain size and shape, lithic and/or mineral makeup,

bed thickness (and how beds are expressed vertically and horizontally), binding surfaces, “bed structure,” bed makeup, sedimentary layers and structures laid down in a particular sequential order, along or within a particular geographic space, during a given time. The second include both lava flow(s) and pyroclastic/tephra sheets, which could be spatially related to the depositional systems.

Both components make up the Basin of México's Wisconsinan lithostratigraphic record, which in principle could be ascertained by means of lithostratigraphic research resulting first in adequately proposed, described, mapped, dated, and correlated formations (or units of lower/higher rank), and subsequently, in the discrimination and characterization of the depositional systems that make them up.

Basin of México's Surface Lithostratigraphic Setting. Here we draw from the information presented in key papers on the geology of this basin that established its lithostratigraphic setting, as currently accepted. There are eight Quaternary epiclastic “formations” proposed for the Basin of México (Bryan, 1948; de Terra, 1948; Arellano, 1951/1953). However, their proposals and descriptions did not meet the stratigraphic and nomenclatorial conventions in use at the time (Ashley et al., 1933), and none has yet been adequately mapped in detail. It follows that such lithostratigraphic units must be regarded as informal. Nonetheless, out of the eight “formations,” these three—“Tarango,” “Tacubaya” and “Becerra Formations” (Bryan, 1948)—merit further consideration, because they subsequently have been widely used in geologic descriptions of this basin. All three “formations” resulted from studies in the basin's western margin.

The “Tarango Formation” is a ~200–300-m-thick fluvial sequence formed by thickly bedded tuffs and volcanoclastic crasso-epiclastics, as well as by thin sheets of pumicite. According to Schlaepfer (1968:fig. 2), this unit occupies the lowest position in the lithostratigraphic column, and unconformably overlies Pliocene volcanic units; in turn it is overlain by or intertongued with Pleistocene volcanic units and unconformably overlain by an alluvial/lacustrine sequence of Pleistocene/Holocene age. The sequence includes the “Tacubaya” and “Becerra Formation” sensu Bryan (1948) and Zeevaert (1953, see below). On the other hand, Arellano (1951/1953:181) interpreted the top of the “Tarango Formation” as the local Pliocene/Quaternary boundary. Later on, Mooser (1961) divided the “Tarango Formation” into lower and upper parts. The upper is largely epiclastic, and unconformably covers the lower part, which is pyroclastic, and thickly bedded.

The “Tacubaya Formation” is defined by a limonitic pedalfers developed in a humid climate, and it is spatially associated with fine-grained epiclastic strata that make up most of the unit's thickness/volume. Stratigraphically, the “Tacubaya Formation” lies above the “Tarango Formation” and below the “Becerra Formation” (Schlaepfer, 1968:fig. 3).

The “Becerra Formation” is also defined by a pedalfers locally developed in an altered humid climate regime; as in the “Tacubaya Formation,” it is spatially associated with fine-grained epiclastic strata that make up the bulk of the unit's volume. At Tequixquiac, México, located ~17 km NW of Zumpango, in the basin's north-central part (see Fig. 4), the “Becerra Formation” has yielded a large vertebrate fauna (Hibbard, 1955).

Basin Of México's Subsurface Lithostratigraphic Setting. Zeevaert (1953), using shallow well information from the western part of the basin, described an at least 170-m-thick fluvio-lacustrine sequence as follows: The lower ~20 m consist of fluvial sediments, covered by an undescribed paleosol (at ~150 m depth), followed upward by an alternation of lacustrine (claystone) and fluvial (sandstone/siltstone) sediments; the lowest strata are very coarse. This in turn is covered by fluvial sediments designated *Tarango Sand II*, overlain by lake sediments consisting of highly compressible montmorillonitic clay bearing diatoms

and ostracods, interbedded by thin ash-fall tuff sheets, in turn covered by well-indurated, calcite-cemented sandstone designated *Tarango Sand I*, which is overlain by 30 m of friable, largely fluvial sediments.

On the other hand, Schlaepfer (1968), based on her unpublished “Report of the Texcoco 1 Deep Well” (later included in SHCP, 1969; *maximal depth reached, ~1650 m; drilled in the Basin’s eastern part*), mentioned that between depths of 180–450 m lies a sequence formed by sand and gravel strata interbedded by thin sheets of tuff and pumice, and by basalt flows. In the lower part (at ~450 m depth) marls [sic] and fresh water limestone are present. She assigned this sequence to the “Tarango Formation,” and dated it as Late Pliocene–Pleistocene. Additionally, this author (Schlaepfer, 1968) upheld Fries’s (1960) contention that the “Tarango” is correlative to the “Atotonilco El Alto Formation,” which lies in south-central Hidalgo (see Segerstrom, 1956).

The Quaternary epiclastic sediments that overlie the “Tarango Formation” (i.e., those placed above the 180 m depth level), were assigned by Schlaepfer (1968) to her Late Pleistocene–Holocene *Lacustrine Beds* and *Alluvium units* (the alluvial/lacustrine sequence mentioned above), as quoted below:

Se comprenden en esta unidad las facies lacustres de las formaciones pleistocénicas Tacubaya y Becerra y de las demás de Bryan tales como fueron definidas por Zeevaert (1953:7). (Translation by present authors: “This unit includes the lacustrine facies of the Pleistocene Formations Tacubaya and Becerra, as well as the other units of Bryan, as they were defined by Zeevaert [1953:7].”) Elsewhere this alluvial/lacustrine sequence is also partly overlain by the volcanic lavic Chichinautzin Formation.

Schlaepfer (1968:fig. 2) shows the Lacustrine Beds and Alluvial Unit as mutually intertonguing among themselves, and with Plio-Quaternary volcanic rock units. Figure 3 of the same paper (her acknowledged interpretation of Bryan, 1948, and Zeevaert, 1953, stratigraphic schemes) depicts the marginal and lacustrine facies of the “Tacubaya” and “Becerra Formations.” Both units are placed in the Wisconsinan.

Basin of México’s Lithostratigraphy: Subsequent Developments. In their Basin of México structural and geophysical study, de Cserna et al. (1987) briefly reviewed the stratigraphy, accepting (de Cserna et al.:19, 21) the “Tarango,” “Tacubaya,” and “Becerra Formations” largely as proposed by Bryan (1948), de Terra (1948), and Arellano (1951/1953). They acknowledged though, that none of them have been mapped. Notwithstanding this, Vázquez-Sánchez and Jaimes-Palomera (1989), as well as Enciso de la Vega (1992), accepted de Cserna et al. (1987) position.

Regarding the lack of mapping, Mooser (1975) compiled a 1:200,000 geologic map of the Basin of México, where he discriminated the “Tarango Formation” in the eastern and western parts of the basin, describing them as consisting of “Volcanic fans [sic] containing lahars, ignimbrites, pumicite beds, ash, soils and some fluvial deposits.” Mooser et al. (1996) produced a new Basin of México geologic map with a scale of 1:50,000, differentiating units by lithic composition and age, designating them by acronyms, for example, Qv, Qial; the “Tarango Formation” is the only lithostratigraphic unit recognized as such. Hernández-Espriú et al. (2014) in their hydrological study of the southwestern part of the Basin of México, present a very small-scale geologic map discriminating informal (“chrono-lithic”) units.

Recently, Arce et al. (2015) report the geology of the San Lorenzo Tezonco Deep Well (depth, 2008 m) and surroundings, largely formed by volcanic rock units (“packages”). Comparing and integrating the surface geology information with the well samples, they recognize, from bottom to top, these units: (a) Package Tepoztlán Formation (depth, 2008–875 m; ages, 20.4–13.5 Ma; largely andesite lava flows); (b) Package Sierra de las Cruces (depth, 875–580 m; ages, 5.0–0.9 Ma; andesitic lava flows and dacitic pyroclastics); (c) Package Cerro de la

Estrella-Santa Catarina (depth, 580–70 m; age, 25 ka; basaltic andesite to dacitic lava flows); and (d) Package Lacustrine (depth, 70–0 m; age, post-25 ka; largely lacustrine with subordinate pyroclastics; it is not assigned to a particular lithostratigraphic unit). The differences with Schlaepfer’s well description are evident. Finally, these authors (Arce et al., 2015) also plot these packages on a surface elevation model of Basin of México’s southern part (Arce et al., 2015:fig. 10), where such packages are implicitly referred to as geologic units of an undetermined class (see NACSN, 2010), namely from bottom to top: Sierra de las Cruces, Cerro Estrella, Sierras de Santa Catarina, and Chichinautzin.

Concluding Remarks on the Basin of México’s Lithostratigraphy.

1. The foregoing review shows that in spite of considerable information on the basin’s surface and subsurface, its Quaternary lithostratigraphic makeup and geologic history are far from settled. The units involved are only grossly known; their precise thickness (volume), areal extent, space stratigraphic relationships with adjacent units, and dating remain to be established. The same applies to the Tertiary component.
2. The “Tarango, Tacubaya, and Becerra Formations,” although widely used, remain informal, because their proposals did not meet the stratigraphic norms then accepted (Ashley et al., 1933), nor did subsequent users attempt to fulfill this requirement, conforming it to the corresponding norms (ACSN, 1961, 1970; NACSN, 1983). Therefore, if at present such units are to serve a useful purpose, they must be formally proposed according to the currently acknowledged stratigraphic and nomenclatorial procedures (see NACSN, 2005; Spanish translation, Barragán-Manzo et al., 2010). This must include (a) a thorough description of the unit; (b) discrimination and description of boundaries, both vertical and lateral; (c) discrimination of the unit in a geologic map at the appropriate scale; (d) designation of the type area; and (e) designation and description of the stratotype.
3. The extensive and uncritical use of the North American Pleistocene Glacial Stage Chronology in the Basin of México, a place located thousands of kilometers south from the areas where it was developed, on the basis of a tangible glacial deposition record actually hampered establishing a sound chronological framework where the geologic events/records could confidently be placed. This fact plagued the early studies, which set the still-prevailing stratigraphic interpretation; such a framework has not been established yet.
4. There is a need for an in-depth review of the lithostratigraphy of the basin, redescribing the already known units (including dependable dating) or proposing new units, and/or attempting to use other kind of units, such as the allostratigraphic ones, if they prove to be more appropriate.

PART 3—OTHER WISCONSINAN SITES

Geologic Setting. The following details the geologic setting of Site 2, San Josecito Cave, Nuevo León, SMO, and Site 13, San Miguel Tocuila, Estado de México, TMVB.

San Josecito Cave Site. This includes deposits formed in an extensive cave complex developed by dissolution of limestones in Nuevo León, northern Sierra Madre Oriental. Deposits include fine-grained clastic debris fills, thin pond and fluvial sequences, and a few speleothems (sensu Neuendorf et al., 2005). Following a local lead, this cave complex was initially prospected for vertebrates by Chester Stock (1943, 1948, 1950), and extensively studied afterwards (see Ferrusquía-Villafranca et al., 2010, for a summary review of such studies); the fauna is a sample of the community that lived in the cave surroundings.

Seemingly different taphonomic mechanisms and processes were involved in assembling the fauna. Small mammals such as rodents and

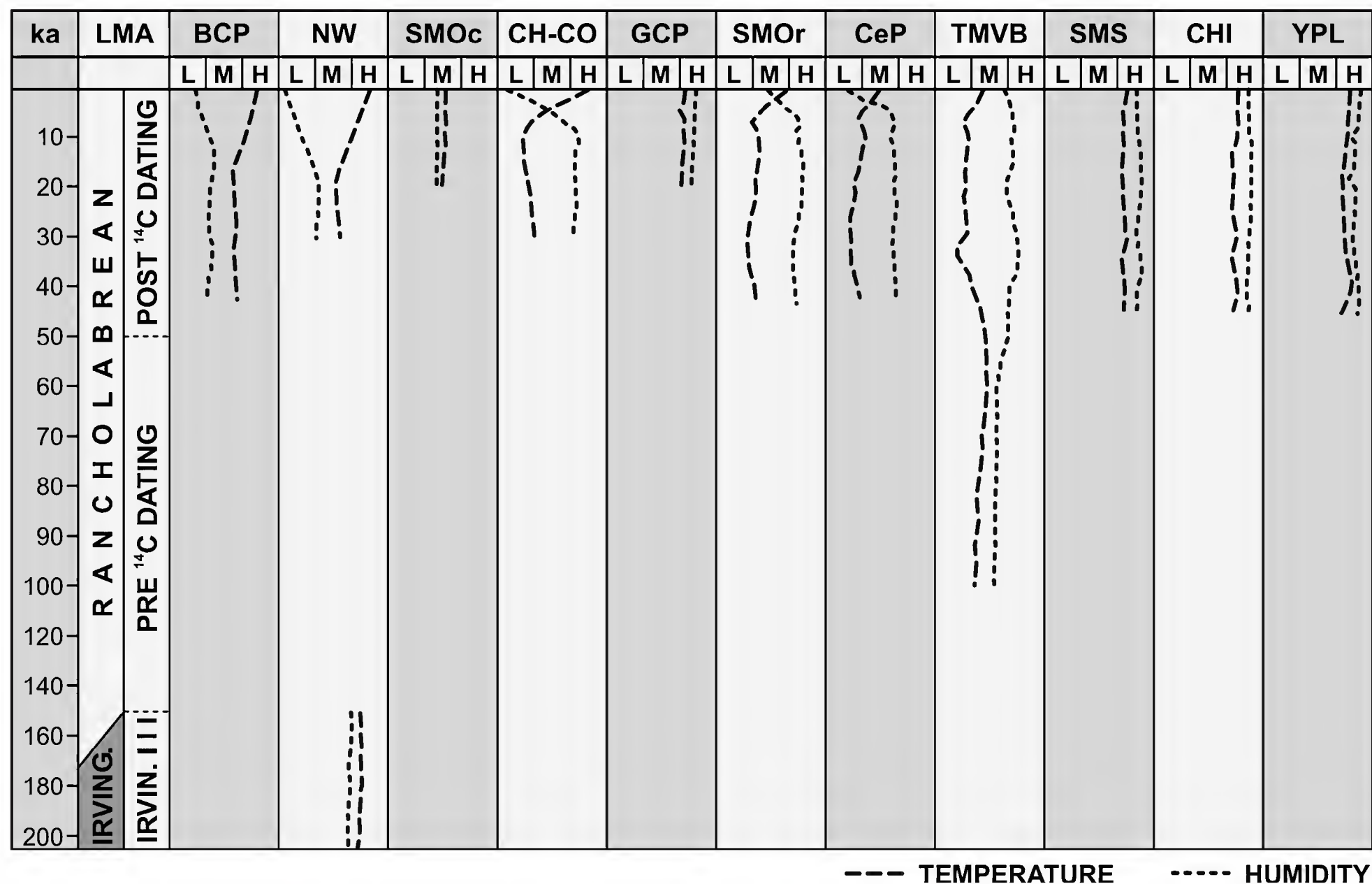


Figure 3 Late Pleistocene probable climate trends in México’s morphotectonic provinces. (Source: Ferrusquía-Villafranca et al. 2010:fig. 16, with permission from Quaternary International/Elsevier). Time frame adapted from Bell et al. (2004). The reviewed palynologic, paleosol, lake sediment, and mammal records/data sets were used to assess the trends. **ABBREVIATIONS:** (from left to right): **L**, Low; **M**, Medium; **H**, High; **LMA**, North American Land Mammal Ages; **BCP**, Baja California Peninsula; **NW**, Northwestern Plains and Sierras; **SMOc**, Sierra Madre Occidental; **CH-CO**, Chihuahuan-Coahuilan Plateaus and Ranges; **GCP**, Gulf Coastal Plain; **SMO**, Sierra Madre Oriental; **CeP**, Central Plateau; **TMVB**, Trans-Mexican Volcanic Belt; **SMS**, Sierra Madre del Sur; **CHI**, Sierra Madre de Chiapas; **YPL**, Yucatan Platform. (For further information pertaining specific data sets used to assess the climatic trends, taxonomic listings of mammal faunas of each morphotectonic province, and/or supplementary references, see Ferrusquía-Villafranca et al., 2010).

chiropterans might have lived there, and were entombed in situ, or they might have been brought in by prey birds. Medium and large mammals might accidentally have fallen through surface fissures and/or holes and, unable to get out, perished there; fallen carcasses might have subsequently become scattered by cave water currents. Finally, it is possible that large predators, for example, bears or wolves, might have used accessible bigger cave areas as temporary or permanent dwellings, bringing in medium to large mammal prey to eat there. Although important advances have been made in the study of this site (see Arroyo-Cabral, 1994), much more work still remains to be done.

San Miguel Tocuila Site. This comprises a lahar deposit bearing numerous mammoth bones (*Mammuthus columbi*, 11.1 ± 0.13 ka, AMS ¹⁴C; Morett et al., 2003) and lies ~40 km ENE from México City Center. The mammoth-bearing layer is a 1.3-m-thick lahar stratum, seemingly derived from loose pyroclastic material laying at high altitude in the Popocatepetl Volcano, placed ~44 km SSE from Tocuila, which was generated during the ~14-ka major eruption, and subsequently removed some 3 ka later, during a warming episode that partly melted the glacier (Siebe et al., 1999). Unfortunately, no detailed geologic map and/or information of the site and surroundings have been presented. The local stratigraphic column, based on the site excavation (Siebe et al., 1999:fig. 3), shows an ~4.5-m-thick succession of pyroclastics and pyroclastic-derived sediments that include the 1.3-m-thick mammoth-

bearing lahar bed, concordantly covered by another 0.68-m-thick lahar bed, on top of which lies a silty-sandy mixture (“loam”) that defines a paleosurface. This is in turn unconformably overlain by a 67-cm-thick lahar bed covered by a 0.34-m-thick hard sand mixture (“loam”), on top of which modern soil has developed.

The stratigraphic column of the same site presented by Morett et al. (2003:fig. 3) differs in the following features from that of Siebe et al. (1999): total thickness of the sequence (~3.6 m versus 4.5 m), interpretation of the fine-grained clastic mixtures (the lower one is a paleosol, and the upper is a caliche layer), thickness of the mammoth-bearing lahar layer [1.7 versus 1.3 m], and location of the lahar source (it came from the Nevado de Toluca Volcano, which lies 98.7 km SW of Tocuila, or from the Popocatepetl). Both Siebe et al. (1999) and Morett et al. (2003) agreed that the lahar flow incorporated already disarticulated mammoth bones (AMS ¹⁴C age of 11.1 ± 0.08 ka; Morett et al., 2003), laying on the ravine surface where the flow traveled. It follows that such flow did not kill the mammoths.

Based on excavations of other parts of the site, Morett et al. (2003:272) claimed that below the mammoth-bearing lahar lies a “complex sequence of volcanic ash, lake silts and laharc deposits,” which does not crop out in the Tocuila site proper, but pinches out just before reaching the site (see Morett et al., 2003:fig. 3). They mentioned that the sequence yields remains of *Equus*, *Bison*, *Camelops hesternus*, and

Table 4 Representative Wisconsinan mammal chronofauna of México as recorded in the chief local faunas. ¹⁴C dated faunas are set in bold. [Modified from Ferrusquía-Villafranca et al., 2010, Tab.12]

	NW	CH-CO		SMOr					CeP	GCP	TMVB					SMS	YPL	
Class Mammalia	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
DIDELPHIMORPHIA																		
Didelphidae																		
<i>Didelphis marsupialis</i>																	X	
<i>Didelphis virginiana</i>				X					X		X							
<i>Mamosa canescens</i>																	X	
<i>Marmosa lorenzoi</i> †																	X	
<i>Marmosa mexicana</i>											X						X	
XENARTHRA																		
Dasypodidae																		
<i>Cabassous centralis</i> ◦																		X
<i>Dasypus novemcinctus</i>											X							
<i>Holmesina septentrionalis</i> †									X		X	X		X				
<i>Pampatherium mexicanum</i> †											X			X	X			
Glyptodontidae †																		
<i>Glyptotherium cylindricum</i> †											sp			X				
<i>Glyptotherium floridanum</i> †												X						
<i>Glyptotherium mexicanum</i> †						X						X						
Megalonychidae †																		
<i>Megalonyx jeffersoni</i> †				X										X				
<i>Megalonyx wheatleyi</i> †				sp		sp							X					
Megatheriidae †																		
<i>Eremotherium laurillardi</i> †											X	X						
<i>Nothrotheriops mexicanum</i> †				X								X						
<i>Nothrotheriops shastensis</i> †				X	X	X	X		X		X	X		X				
Mylodontidae †																		
<i>Paramylodon harlani</i> †						X			X		X	X						
<i>Paramylodon</i> sp. †	sp																	
INSECTIVORA s.l.																		
Soricidae																		
<i>Cryptotis mayensis</i>																	X	
<i>Cryptotis mexicana</i>				X														
<i>Cryptotis parva</i>			X					X										
<i>Notiosorex crawfordi</i>			X															
<i>Sorex milleri</i>				X														
<i>Sorex saussurei</i>				X														
CHIROPTERA																		
Antrozoidae																		
<i>Antrozous pallidus</i> ◦			X															
Emballonuridae																		
<i>Peropteryx macrotis</i>																	X	
Molossidae																		
<i>Eumops bonariensis</i>																	X	
<i>Eumops perotis</i> ◦		X																
<i>Eumops underwoodi</i> ◦																	X	
<i>Molossus rufus</i>																	X	
<i>Nyctinomops laticaudatus</i>																	X	
<i>Promops centralis</i>																	X	
<i>Tadarida brasiliensis</i>			X															
Mormoopidae																		
<i>Mormoops megalophylla</i>				X	X								X				X	X
<i>Pteronotus davyi</i>																	X	
<i>Pteronotus parmallii</i>																	X	X
Natalidae																		
<i>Natalus stramineus</i>																	X	
Phyllostomidae																		
<i>Artibeus jamaicensis</i>																	X	X
<i>Artibeus lituratus</i>																	X	
<i>Carollia brevicauda</i>																	X	
<i>Centurio senex</i>																	X	
<i>Chiroderma villosum</i>																	X	
<i>Choeronycteris mexicana</i>				X														
<i>Chrotopterus auritus</i>																	X	X
<i>Desmodus</i> cf. <i>D. draculae</i> †																	X	
<i>Desmodus rotundus</i>										X							X	
<i>Desmodus stocki</i> †				X	X	X							X					

Table 4 Continued.

	NW	CH-CO		SMOr					CeP	GCP	TMVB					SMS	YPL	
Class Mammalia	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
<i>Diphylla ecaudata</i>																	X	
<i>Glossophaga soricina</i>																	X	
<i>Leptonycteris curasoae</i>					X													
<i>Leptonycteris nivalis</i>				X														
<i>Macrotus californicus</i> ◦					X													
<i>Mimon bennettii</i>																		X
<i>Sturnira lilium</i>																	X	
Vespertilionidae																		
<i>Corynorhinus townsendii</i>				X														
<i>Eptesicus brasiliensis</i>																		X
<i>Eptesicus furinalis</i>																		X
<i>Eptesicus fuscus</i>				X													X	
<i>Lasiurus cinereus</i>				X														
<i>Lasiurus ega</i>																	X	
<i>Lasiurus intermedius</i>																	X	
<i>Myotis californicus</i>				X														
<i>Myotis keaysi</i>			sp		sp	sp											X	
<i>Myotis thysanodes</i>				X														
CARNIVORA																		
Canidae																		
<i>Canis cedazoensis</i> †									X									
<i>Canis dirus</i> †				X		X	X		X		X	X		X			X	
<i>Canis familiaris</i>										X	X			X			X	
<i>Canis latrans</i>		X	X	X	X	X			X		X	X	X	X			X	
<i>Canis lupus</i>				X		X	X	X			X	X		X				
<i>Canis rufus</i> •						X						X						
<i>Cuon alpinus</i> •				X														
<i>Urocyon cinereoargenteus</i>		X		X	X				X								X	
Felidae																		
<i>Herpailurus yagouaroundi</i>				X													X	
<i>Leopardus pardalis</i>																		X
<i>Lynx rufus</i>		X	X	X				X	X			X	X					
<i>Panthera atrox</i> †	X			X					X		X	X						
<i>Panthera onca</i>	X	X		X				X	X									
<i>Puma concolor</i>		X	X	X						X	X					X	X	
<i>Smilodon fatalis</i> †				X					X		X	X						
<i>Smilodon gracilis</i> †														X				
Mustelidae																		
<i>Conepatus leuconotus</i>										X								
<i>Conepatus mesoleucus</i>		X		X							X							
<i>Lontra longicaudis</i>											X		X					
<i>Mephitis mephitis</i>		X		X									X					
<i>Mustela frenata</i>				X	sp												X	
<i>Mustela nigripes</i> ◦			X															
<i>Spilogale putorius</i> ◦		X		X	X												X	X
<i>Taxidea taxus</i>		X		X					X				X	X				
Procyonidae																		
<i>Bassariscus astutus</i>	X	X		X													X	
<i>Bassariscus ticuli</i> †					X													
<i>Nasua narica</i>		X															X	
<i>Procyon lotor</i>		X									X		X					X
Ursidae																		
<i>Arctodus pristinus</i> †									X			X		X				
<i>Arctodus simus</i> †						X			X		X	X		X				
<i>Tremarctos floridanus</i> †				X														
<i>Ursus americanus</i> ◦		X	X	X		X						sp	X					
RODENTIA																		
Cuniculidae																		
<i>Cuniculus paca</i>																	X	
Erethizontidae																		
<i>Erethizon dorsatum</i> ◦		X		X	X				X									
<i>Coendou mexicanus</i>																	X	
Geomyidae																		
<i>Cratogeomys castanops</i>		X	X	X		X		X	X			X	X					
<i>Cratogeomys gymnurus</i>											X							
<i>Cratogeomys merriami</i>													X					

Table 4 Continued.

[illegible]

Table 4 Continued.

	NW	CH-CO		SMOr					CeP	GCP	TMVB					SMS	YPL	
Class Mammalia	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
LAGOMORPHA																		
Leporidae																		
<i>Aztlanolagus agilis</i> †			X															
<i>Lepus alleni</i>								sp										
<i>Lepus californicus</i>		X	X		X	X	X											
<i>Sylvilagus audubonii</i>		X	X		X	X	X	sp			sp							
<i>Sylvilagus brasiliensis</i>																	X	
<i>Sylvilagus cunicularius</i>					X								X					
<i>Sylvilagus floridanus</i>				X	X	X							X				X	
<i>Sylvilagus leonensis</i> †				X	X			X										
PERISSODACTYLA																		
Equidae ♦																		
<i>Equus calabatus</i> †									X				X					
<i>Equus conversidens</i> †	sp		sp	X	sp	X	X	sp	X		X	X		X			X	
<i>Equus excelsus</i> †									X			X		X				
<i>Equus giganteus</i> †												X						
<i>Equus mexicanus</i> †						X					X	X	X	X				
<i>Equus occidentalis</i> †							X					X		X				
<i>Equus pacificus</i> †						sp			X			X						
<i>Equus parastylidens</i> †									X									
<i>Equus tau</i> †	X											X						
Tapiridae																		
<i>Tapirus bairdii</i> ◦											sp	sp		X				
<i>Tapirus haysii</i> †				X		X	X											
ARTIODACTYLA																		
Antilocapridae																		
<i>Antilocapra americana</i>		X	X				X											
<i>Capromeryx mexicana</i> †			sp		sp	X			X	X		X						
<i>Capromeryx minor</i> †	X																	
<i>Stockoceros conklingi</i> †				X	X			X	X	X		X		X	X			
<i>Tetrameryx mooseri</i> †	sp								X			sp						
<i>Tetrameryx shuleri</i> †										X	X			X	X			
<i>Tetrameryx tacubayensis</i> †									X									
Bovidae																		
<i>Bison alaskensis</i> †	sp					sp			X		X	X		X				
<i>Bison antiquus</i> †										X	X	X		X				
<i>Bison bison</i> ◦		X															X	
<i>Bison latifrons</i> †											X	X	X					
<i>Bison priscus</i> †							X											
<i>Euceratherium collinum</i> †				X		X						X						
<i>Oreamnos harringtoni</i> †				X														
<i>Ovis canadensis</i> ◦		X																
Camelidae ♦																		
<i>Camelops hesternus</i> †	X					X	X		X		X	X	X	X	X			
<i>Camelops mexicanus</i> †												X						
<i>Camelops minidokae</i> †														X				
<i>Camelops traviswhitei</i> †					X				X									
<i>Eschatius conidens</i> †												X						
<i>Hemiauchenia blancoensis</i> †					sp				sp				sp				sp	
<i>Hemiauchenia macrocephala</i> †						X	X					X		X				
<i>Hemiauchenia vera</i> †						X												
<i>Procamelops minimus</i> †															X			
Cervidae																		
<i>Cervus elaphus</i> •		X										sp						
<i>Mazama americana</i>										X							X	
<i>Navahoceros fricki</i> †				X					X							X		
<i>Odocoileus halli</i> †						X			X			sp	X					
<i>Odocoileus hemionus</i>	X	X						X			X							
<i>Odocoileus virginianus</i>		X			X		X			X			X				X	X
Tayassuidae																		
<i>Platygonus alemanii</i> †				sp					sp									
<i>Platygonus compressus</i> †												X		X				
<i>Platygonus ticuli</i> †						X					X							
<i>Tayassu tajacu</i>												sp					X	X

Table 4 Continued.

	NW	CH-CO		SMOr					CeP	GCP	TMVB					SMS	YPL	
Class Mammalia	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
PROBOSCIDEA																		
Elephantidae ♦																		
<i>Mammuthus columbi</i> †	sp					sp	X		sp		X	X	sp	X				
<i>Mammuthus primigenius</i> †											X	X						
Gomphotheriidae †																		
<i>Cuvieronius tropicus</i> †											sp	X		sp				
<i>Stegomastodon</i> cf <i>S. mirificus</i> †											X	X						
Mammutidae †																		
<i>Mammut americanum</i> †						sp	sp		X		sp	X		X			X	
?LITOPTERNA †																		
?Macrauchenidae †																X		
Gen. et sp. indet. †																X		

Source: Modified from Ferrusquía-Villafranca et al. (2010, Tab. 12).
Symbology: † Extinct taxon. ♦ Suprageneric taxon extinct in Mexico, but extant outside Mexico. * Species extinct in Mexico, but extant outside this country. ○ Species extinct in the morphotectonic province(s) bearing the fossil locality(ies), but extant elsewhere in Mexico. X = Recorded species in a local fauna. sp = Recorded genera in a local fauna, but species is undetermined.
Morphotectonic Province Abbreviations: NW, Northwestern Plains and Sierras. CH-CO, Chihuahuan-Coahuilan Plateaus and Ranges. SMOr, Sierra Madre Oriental. CeP, Central Plateau. GCP, Gulf Coast Plain. TMVB, Trans-Mexican Volcanic Belt. SMS, Sierra Madre del Sur. YPL, Yucatan Platform.
Local Faunas: A, La Brisca, Son. B, Cuatro Ciénegas, Coah. C, Cueva Jiménez, Chih. D, San Josecito, NL. E, La Presita, SLP. F, El Cedral, SLP. G, Minas, NL. H, Mina San Antonio, SLP. I, El Cedazo, Ags. J, Mixtequilla, Ver. K, Chapala-Zacoalco, Jal. L, Tequixquiac, Mex. M, Tlapacoya, Mex. N, Valsequillo, Pue. O, Hueyatenco, Pue. P, San Agustín, Oax. Q, Gruta de Loltún, Yuc. R, Actún Spukil, Yuc.

Sylvilagus cunicularius. Unfortunately though, Morett et al. (2003) did not thoroughly describe this sequence, its stratigraphic spatial relationships along the excavated places, or the geology of the site and surroundings. Further, they (Morett et al., 2003) did not elaborate on the purported Nevado de Toluca lahar-flow provenance.

It should be noted that neither Siebe et al. (1999) nor Morett et al. (2003) explain the enormous mammoth bone concentration (including the seven carcasses mentioned above) in a mere 28-m² area (Siebe et al., 1999:1550, fig. 2; Morett et al., 2003:fig. 2). On the other hand, González et al. (2001:705) proposed that the seven mammoths present in Tocuila were probably killed by an eruption of the Nevado de Toluca that took place ca. 11.6 ka, and that shortly after, a lahar flow from the same volcano picked up the *Mammuthus columbi* carcasses and moved them a short distance to Tocuila. Although they mentioned that the lahar included tephra from different sources—Popocateptl ca.14 ka, Tutti Frutti (= PWA) and Gray Pumice (~70.7 % SiO₂ content), and Nevado de Toluca Pumice (ca. 11.6 ka, ~61 % SiO₂ content)—they did not discuss proportions of each source in the tephra, or the mixing mechanisms.

Subsequently González et al. (2014, 2015) restudied in detail the Tocuila site, describing the ~4.0-m-thick trench exposure as a fine-clastics (largely clay and silt) lake sequence intercalated by pyroclastic and/or tephra sheets. These were unconformably overlain by a channel lahar infill ~1.3 m thick, seemingly formed by four beds with convoluted top and bottom surfaces, the lower part of which yielded the mammoth bones (González et al., 2014:fig. 6). The mammoth bones yielded AMS ¹⁴C ages of 11,100 ± 80 years BP to 11,255 ± 75 years BP (see González et al., 2003). The fossil accumulation is thought to be the result of lahar funneling through a narrow channel. However, the fossil:lahar volume ratio preserved, roughly 1:4 at least (see González et al., 2014:fig. 6a), seems rather low to have accomplished this fossil removal and concentration.

The sequence below the lahar deposit includes GBA and PWA bed markers respectively 28,600 ± 200 years BP and 14,600 ± 65 years BP, the former is reworked and was identified by its geochemical makeup. There is also a 10-cm layer that contains Fe spherules (~0.065 mm), and microtektite particles (smaller than the spherules), which have

been interpreted as evidence of an airburst meteorite (González et al., 2014, 2015). Similar evidence has also been detected in Lake Cuitzeo beds, Michoacán (Israde-Alcántara et al., 2012), and in South America (Firestone et al., 2007). This airburst meteorite occurred close to the Younger Dryas cooling event, and is interpreted as a possible cause of the Late Pleistocene megafaunal extinction; this hypothesis has not gone unchallenged (Haynes, 2008; Scott et al., 2010).

RADIOMETRIC/BIOCHRONOLOGIC DATING AND REGIONAL SIGNIFICANCE: MÉXICO’S WISCONSINAN CHRONOFAUNA

The radiometric data of the Wisconsinan sites are presented in Table 1, and were largely discussed above (see above, “Chronological Spread of the Sites”). All sites bear vertebrate faunas; their individual diversity varies greatly but they have considerable taxonomic overlap (i.e., shared taxa), as would be expected from chronologically similar faunas. The “major” faunas belong to Sites 2, San Josecito Cave, Nuevo León; 3, El Cedral, San Luis Potosí; 9, Tlapacoya (including 10, Tlapacoya I), Estado de México; and 17, Valsequillo, Puebla; taken together, these sites display a wide geographic spread and could confidently be used to draw a meaningful characterization/representation of México’s Wisconsinan chronofauna (Table 4, modified from Ferrusquía-Villafranca et al., 2010:fig. 16). The chronofauna includes the following taxa: Didelphimorphs (“possums;” Didelphidae, only in San Josecito Cave, hereafter SJC), Dasypodidae (only in Tlapacoya), Pampatheriidae (only in Tlapacoya), Glyptodontidae (absent in SJC), Megalonychidae (only in El Cedral), Megatheriidae (only in El Cedral), Mylodontidae (only in El Cedral), Soricidae (only in SJC), Mormopidae (only in SJC and Tlapacoya), Phyllostomatidae (only in SJC, and Tlapacoya), Vespertilionidae (only in SJC), Canidae (only in Tlapacoya and Valsequillo), Felidae (only in Tlapacoya and Valsequillo), Mustelidae (only in Tlapacoya and Valsequillo), Procyonidae (only in Tlapacoya), Ursidae (present in all major faunas), Erethizontidae (only in SJC), Geomyidae (only in SJC and Tlapacoya), Heteromyidae (only in SJC and Tlapacoya), Hydrochoeridae (only in Tlapacoya), Muridae (only in SJC), Sciuridae (only in SJC), Leporidae (absent in Valsequillo), Equidae (absent in Valsequillo), Tapiridae (absent in Valsequillo),

Antilocapridae (absent in Tlapacoya), Bovidae (absent in SJC), Camelidae (absent in SJC), Cervidae (absent in Valsequillo), Tayassuidae (absent in Tlapacoya), Elephantidae (absent in SJC), Gomphotheriidae (only in Valsequillo), and Mammutidae (absent in SJC).

The taxonomic composition of this chronofauna, includes Asian immigrants long established and differentiated in temperate North America (e.g., proboscideans, bovids), South American late-comers (e.g., xenarthrans and hydrochoerid rodents), and Late Cenozoic indigenous North American taxa (e.g., insectivores, sciurids, equids, and canids) and has a characteristic Wisconsinan outlook (see Bell et al., 2004). On this basis, it is assigned to the Wisconsinan SubNALMA, an age assignment well supported by the associated radiometric data (see Table 1).

Environmental Significance of the Wisconsinan Fauna of México

Locally, this chronofauna shows tropical taxa (e.g., vampire bats, most xenarthrans, hydrochoerids) and temperate taxa (e.g., insectivores, antilocaprids, sciurid rodents, leporids) coexisting side by side. Present-day mammal faunas have an ecologically and biogeographically harmonious composition, whereas that of the Pleistocene faunas are disharmonious (Bell et al., 2004), and evidence significant ecologic and biogeographic shifts of the component taxa, which are related to major Late Pleistocene/Early Holocene environmental changes. This subject is further developed in Ferrusquía-Villafranca et al. (2010).

México's Wisconsinan chronofauna is strikingly different from that of the Holocene (Ceballos and Oliva, 2005) by the presence of large-sized mammals, for example, equids, proboscideans, the majority of carnivores, xenarthrans, artiodactyls, and hydrochoerids, or the extirpation of others, for example, tapirs and phyllostomatid vampire bats that today characterize tropical regions. The Wisconsinan fauna was much more diverse at higher taxon level (e.g., family and order) than the Holocene one (Ferrusquía-Villafranca et al., 2010). Thus, the Holocene fauna of México is a taxonomically impoverished version of its Wisconsinan counterpart, and small-sized mammals overwhelmingly dominate. This phenomenon is part of the worldwide major extinction that took place by terminal Pleistocene–Early Holocene time (ca. 10 ka), a subject much discussed, but not yet settled (see Martin and Klein, 1989; Firestone et al., 2007).

These differences attest to the profound environmental changes that occurred at the Wisconsinan/Holocene “transition,” a matter still widely discussed by many authors (see Urrutia-Fucugauchi et al., 1997, and literature therein; Caballero-Miranda et al., 1999, 2002; Metcalfe et al., 2000; Lozano-García et al., 2005). On the other hand, Ferrusquía-Villafranca et al. (2010) employed a multidisciplinary approach, using mammal species, palynomorphs/palynofloras, paleosol features, and lake sedimentary records (both physical and biotic) as climatic and environmental indicators to show that (a) the limited and strongly time/space-biased available information across the country only allows one to portray broad countrywide climatic/environmental changes (i.e., trends, see Ferrusquía-Villafranca et al., 2010:fig. 16, here reproduced as Fig. 4); (b) the necessary dependable, discipline-specific, countrywide data sets/databases require much additional work across the country; such effort is anticipated to extend many years into the future to complete the existing databases, for example, geologic s.l (stratigraphic and sedimentological), radiometric-geochronologic, and magneto-geochronologic studies; development of stable isotopes (for establishing “absolute” paleothermal parameters); studies of paleosols (as climatic indicators); and paleontological sensu lato studies (largely on palynomorphs and vertebrates as biotic components and climatic indicators); and (c) parsimonious integration of the discipline-specific data sets/databases through multidisciplinary and interdisciplinary research, from

which the environmental change occurred since the Wisconsinan, could accurately and quantitatively be portrayed for México as a whole.

BEARING OF THE WISCONSINAN CHRONOFAUNA ON THE PEOPLEING OF MÉXICO/THE AMERICAN CONTINENT

México's Wisconsinan record holds two of the earliest occurrences of humans in the American continent based on direct human skeletal material, namely those of the Peñón III (Site 16) and Tlapacoya I (Site 10), Mexican Basin, TMVB MP, central México, which respectively yielded AMS ^{14}C ages of 10.775 ka and 10.21 ka (González et al., 2003). Further, the lithic tools found within tephra layers in the Santa Isabel Ixtapan (Site 4), dated between 14.5 and 10.8 years BP (see Table 1), suggest even earlier dates for human occupation in the Basin of México.

Comparable South American early human records are not older than 9.72 ka (Neves and Pucciarelli, 1991). The older (12.5-ka) Chilean human habitation Monte Verde site was not dated on human skeletal material (Dillehay, 1989). Thus, the Mexican Basin human records are older than those of South America, being quasi-contemporaneous with the Clovis people of southwestern United States, who lived ca. 11.5 ka, and with other records based on human skeletal material from North America include those of Arlington Springs, Santa Rosa Island, California (10.96 ± 0.08 ka, Johnson et al., 2000), and Buhl, Idaho (10.675 ± 0.95 ka, Green et al., 1998).

Certainly, there are claims for earlier records of humans in México, for example, those of Tlapacoya (Site 9, dated at 35 to 21.7 ka; Lorenzo and Mirambell, 1986b); or the purported 40-ka human footprints from Valsequillo (González et al., 2006). In the very interesting archaeological/paleontological Tlapacoya site, vertebrate fossils are associated with coarse-grained clastic strata that bear pebble-like, “faceted” objects interpreted as human-made artifacts (“tools”), as well as charcoal, organic matter, and hearths thought to be human-generated and dated by standard-method ^{14}C yielding ages ~ 24 ka. Unfortunately, little if any stratigraphic detail of the dated material-bearing strata was furnished. Outside México, the reported dates of such an early presence of humans in the American continent have been met with skepticism, which is based on methodological and stratigraphic caveats (González et al., 2001). Further, new local stratigraphic studies (González et al., 2015) yielded no evidence to support such age. Therefore, the Peñón III and Tlapacoya I records based on direct human skeletal material remain as the earliest (10.755 ± 0.075 ka, and 10.2 ± 0.065 ka, respectively) undisputed evidence of humans in México.

CONCLUSIONS

1. The combined radiometric and paleontological approach has improved biochronology, allowed dependable and more precise long-range correlation, and been the driving force behind a qualitative leap in understanding Earth's geologic history and evolution. Even so, this approach is still not widely used in México despite its early start. Here we report 21 sites where this approach was applied. Their space and time distribution is quite uneven, omitting many morphotectonic provinces (BCP, SMOc, CH-CO, CeP, GCP, and YP) and geochronologic intervals, for example, Irvingtonian and Early Rancholabrean. The combined space and time spread (Table 1) shows this arrangement of sites: NW, one Early Rancholabrean; SMOc, two Late Rancholabrean; TMVB, one Irvingtonian and 13 Rancholabrean; SMS, two Rancholabrean; and SMCh, two Irvingtonian. Patchiness or skewness aside, the results from the sites' geologic setting and fossil content are quite significant.

2. The 21 Pleistocene sites dealt with here (from NW, one; SMOr, two; TMVB, 14; SMS, two; and SMCH, two) disclose the need to describe or revise their lithostratigraphic settings. However, despite current limitations in their lithostratigraphic documentation, they are of prime importance for understanding the Quaternary environmental change (climatic and otherwise, including timing, extent, and biotic impact). Their mammal assemblages belong to three chronofaunas: Irvingtonian (three records) and Early Rancholabrean (one record), and very Late Rancholabrean (Wisconsinan; 17 records). During this interval, the fauna underwent a profound change through time and space, drastically modifying its taxonomic makeup, its biogeographic distribution, and its entire physiognomy with a strong trend toward losing meso- and megabaryc taxa, taxonomic depauperation (by means of selective extinction/expatriation), and biogeographic shuffling. Thus, the Holocene fauna is an impoverished version of its Pleistocene counterpart. Finally, during this epoch our own species appears in México. In fact some of the oldest records of humans based on direct dating of human skeletal material are from this country.
3. The present study documents 21 sites with radiometric dates and studied vertebrate assemblages. The stage is set to extend this methodology to other Pleistocene localities throughout the country; this would considerably improve our understanding of México's Late Cenozoic biotic and geologic history and evolution.

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LATE CRETACEOUS OYSTERS FROM THE PACIFIC SLOPE OF NORTH AMERICA: REVISION OF NAMED SPECIES AND DISCOVERY OF NEW SPECIES¹

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ABSTRACT. Late Cretaceous oyster species are common faunal components in shallow-marine siliciclastic rocks on the Pacific slope of North America (PSNA), in a region extending southward from Vancouver Island, British Columbia, Canada, to Northern Baja California, Mexico. Seven species have been named, but they are poorly known. The purpose of this study is to better document these species by upgrading their morphologic, taxonomic, geographic, and stratigraphic data. In addition to the seven revised species, four new species, a questionable species, and an unnamed species were detected, resulting in a total of 13: *Oscillopsa popenoei* sp. nov.; *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825); *Curvostrea crescentica* (Packard, 1922); *Curvostrea baia* sp. nov.; *Acutostrea taxidonta* (Packard, 1922); *Crassostrea breweri* (Gabb, 1864); *Costagrya californica* (Packard, 1922); *Costagrya garza* sp. nov.; *Amphidonte parasitica* (Gabb, 1864) [assignment to this genus by Elder (1991) is confirmed]; ?*Amphidonte parasitica* (Gabb, 1864); *Pycnodonte (Pycnodonte) malleiformis* (Gabb, 1864); *Phygraea inornata* (Packard, 1922); and *Phygraea arida* sp. nov. Morphs most likely represent ecophenotypic responses to different water energies (e.g., *A. taxidonta*) or whether or not there was attachment (e.g., *P. inornata*). Growth stages were newly recognized for *A. parasitica*.

None of the detected oyster genera or subgenera are endemic to the warm-temperate PSNA region. Except for *Amphidonte*, none were previously recognized in the Cretaceous record of the PSNA region. The late Santonian *Oscillopsa popenoei* is the first occurrence of this genus in North America. The highest biodiversity level of PSNA oyster species (five) coincided with the Turonian and late early to early late Maastrichtian (both warm times with high sea level), and the lowest biodiversity level (zero) coincided with the Coniacian (cooler time with lower sea level). In the PSNA region, there was a reoccurrence of the Turonian *Curvostrea*-*Costagrya*-*Phygraea* association in the late early to early late Maastrichtian.

INTRODUCTION

Oysters are common in Upper Cretaceous shallow-marine strata in the region extending from Vancouver Island, British Columbia, Canada, to Northern Baja California, Mexico (Fig. 1), referred to hereafter as PSNA (Pacific Slope of North America). Seven species have been named. Gabb (1864) named three, based on collecting in Northern California, and Packard (1922) named four, based on collecting in Southern California. Their descriptions are inadequate because they are too brief and rely on only the holotype. Their illustrations are commonly insufficient because they show only one view of a badly weathered holotype or show only its interior. In addition, Gabb's illustrations are idealized sketches. Subsequent workers encountered difficulty in trying to recognize these species and generally avoided using Gabb's and Packard's names, as evidenced by the short synonymies given here.

The purpose of this study is to improve on the fundamental paleontologic information concerning these previously named species. The improvements include 1) more detailed morphologic descriptions, including recognition of morphs and xenomorphism, 2) all the photographs necessary to document the observed morphologies, 3) integration of current concepts of familial classification of oysters, 4) integration of more comprehensive geographic and stratigraphic distributions, and 5) updated chronostratigraphic data. During the course of this study, four new species, one unnamed species, and one questionable species were also discovered. The revisions and these new discoveries have allowed, for the first time, meaningful biodiversity information concerning the oyster fauna to be inferred. The significance

of this contribution is that it establishes a modern foundation for future studies of Late Cretaceous PSNA oysters.

MATERIALS AND METHODS

The collection at the Natural History Museum of Los Angeles County, Invertebrate Paleontology (LACMIP) Department, is the principal source of material. Two of the core strengths of the collection's Cretaceous holdings are 1) Turonian through Campanian fossils collected by W.P. Popenoe and L.R. Saul in the Santa Ana Mountains, Orange County, California, and 2) Turonian fossils collected by W.P. Popenoe in the Redding area, Shasta County, California. The specimens they collected are critical for the revisions reported here. More recent additions of well preserved fossils to the LACMIP collection were essential in confirming and expanding the work of Elder (1991) on *Amphidonte parasitica* (Gabb, 1864).

Specimens from British Columbia, Canada, were the sources for supplemental material. Although Cretaceous strata are plentiful along the southeast side of Vancouver Island, British Columbia, oysters are not common in these strata, except at a few localities, like near Nanaimo (Ludvigsen and Beard, 1994, 1997) and on western Denman Island (R. Graham, personal communication, 2015). Raymond Graham facilitated the loan of some Nanaimo material collected by Graham Beard and now part of the Vancouver Island Paleontological Museum (VIPM) collection in Qualicum Beach, British Columbia. Raymond Graham photographed these specimens and provided detailed stratigraphic information. Raymond Graham also lent some western Denman Island specimens collected by him and Timon Bullard. Two of R. Graham's specimens and one of T. Bullard's specimens are used here as paratypes of *Phygraea arida* sp. nov. These three specimens are now part of the Royal British Columbia Museum (RBCM) collection in Victoria, British Columbia, Canada.

Upper Cenomanian oysters occur predominantly as internal casts, whereas Turonian through upper Maastrichtian oysters are generally

¹ URL: www.nhm.org/scholarlypublications

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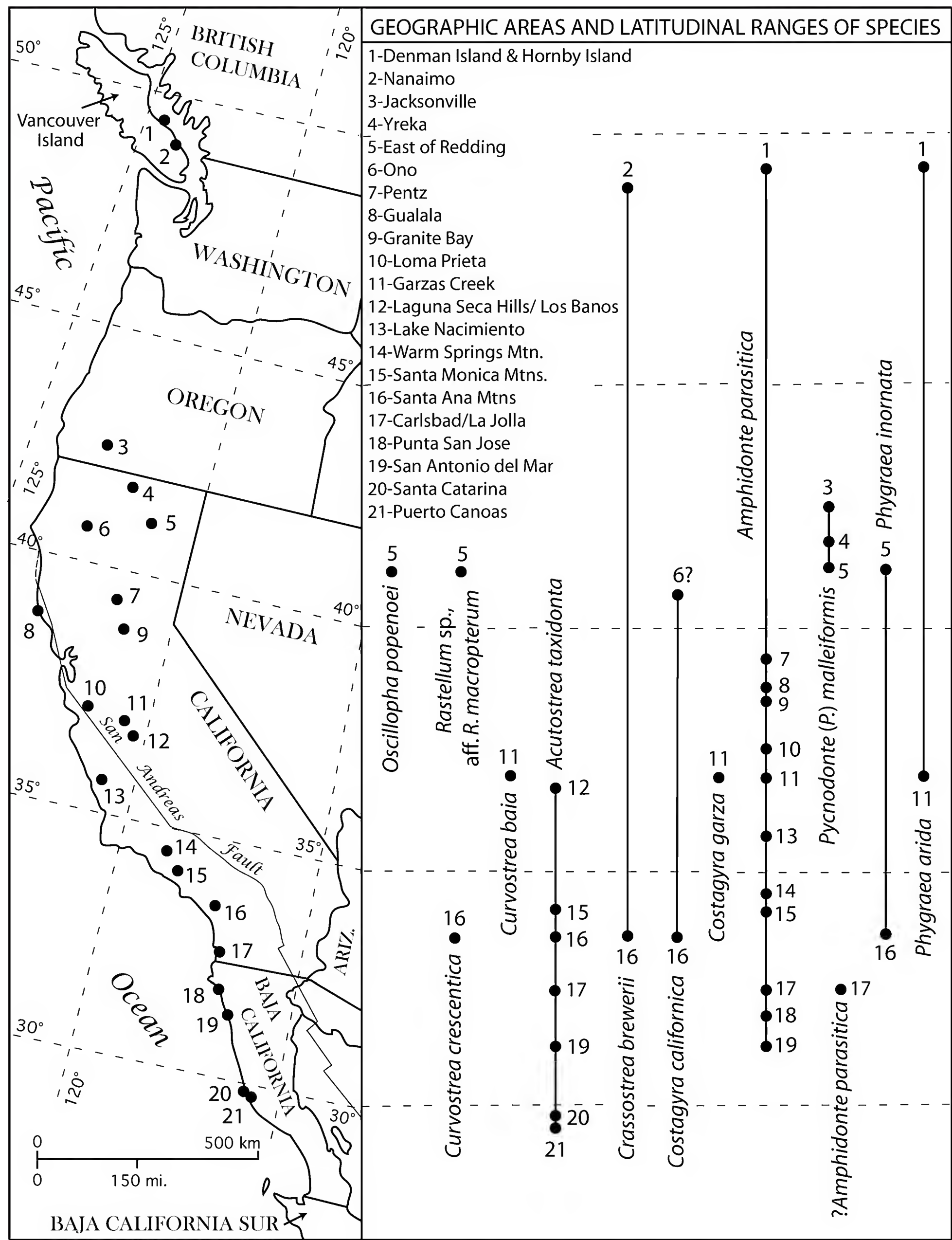


Figure 1 Geographic areas and latitudinal distribution of PSNA Late Cretaceous oyster species.

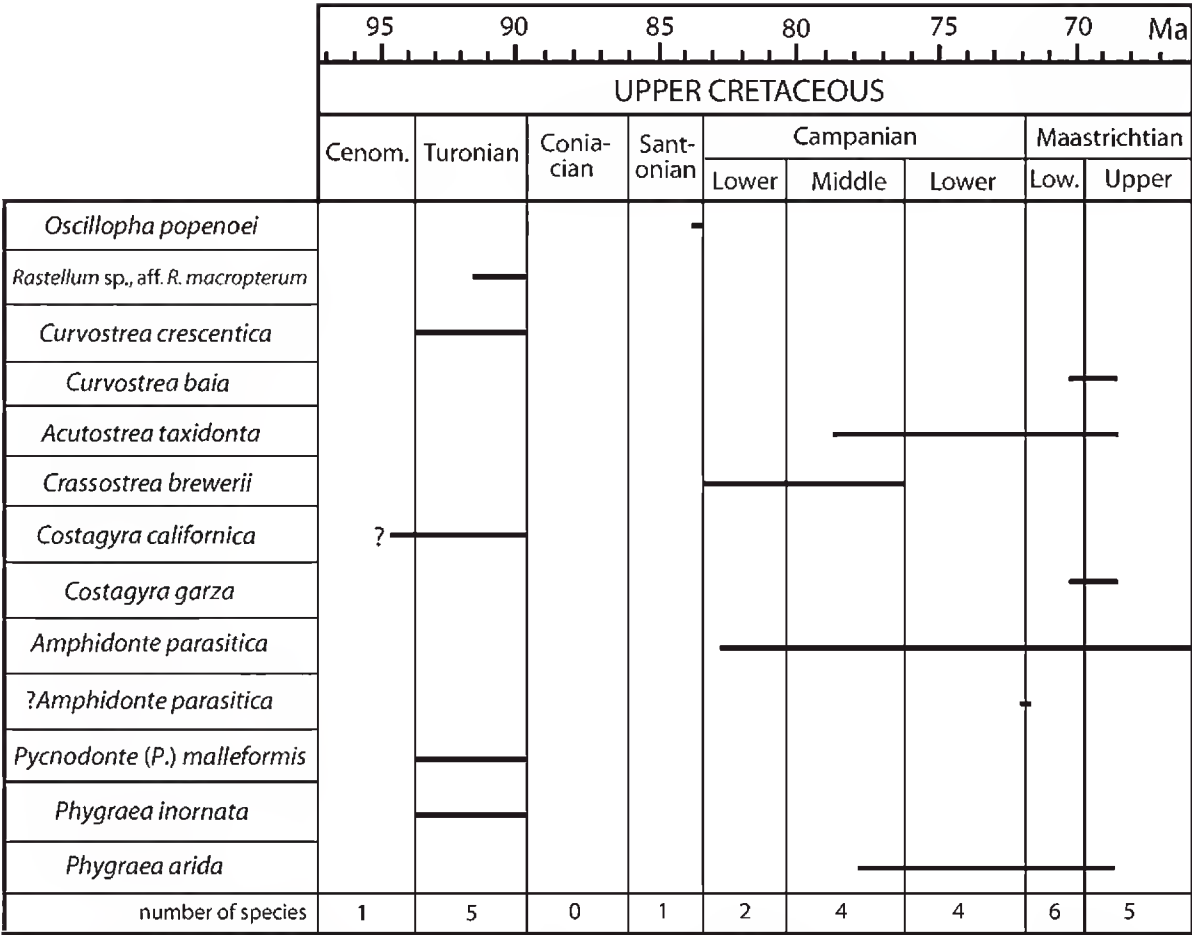


Figure 2 Chronostratigraphic ranges of PSNA Late Cretaceous oyster species and number of species per stage. Ages of stage boundaries from Gradstein et al. (2012).

well preserved. No confirmable Coniacian oysters were detected. Uppermost Maastrichtian oysters are poorly preserved.

The examined specimens are nearly all from shallow-marine siliciclastic deposits, consisting commonly of siltstone or silty fine-grained sandstone. In rare cases, the shallow-marine oysters experienced postmortem transport via turbidity currents into deeper environments. “Area” designations (see Fig. 1) for where the oysters were found are used throughout the text. Current summaries of the geological details of the formations and members containing the studied oysters are in the following papers (listed in ascending chronostratigraphic order): Budden Canyon Formation, Bald Hills Member (Squires and Saul, 2004) [Area 6]; Hornbrook Formation, Osburger Gulch Member (Squires and Saul, 2003a) [Area 4]; Redding Formation, Bellavista Sandstone Member, Frazier Siltstone Member, and Member VI (Squires and Saul, 2003b) [Area 5]; Ladd Formation, Baker Canyon Member (Saul and Squires, 2003) and Holz Shale Member (Squires and Saul, 2001) [Area 16]; Haslam Formation (Squires and Saul, 2001) [Area 2]; Chico Formation at Granite Bay (= Texas Flat) (Squires and Saul, 2009) [Area 9]; Chico Formation at Pentz (Squires and Saul, 2001) [Area 7]; Cedar District Formation, “White House” site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada (Squires and Saul, 2006a; Ward et al., 2015) [Area 1]; upper Tuna Canyon Formation (Squires and Saul, 2009) [Area 15]; unnamed formation, Loma Prieta (Elder, 1991) [Area 10]; Williams Formation, Pleasants Sandstone Member (Squires and Saul, 2001) [Area 16]; Point Loma Formation (Squires and Saul, 2001) [Area 17]; Rosario Formation (Squires and Saul, 2001; Ward et al., 2015) [Areas 18–21]; Northumberland Formation, Collishaw Point, Hornby Island, off the east coast of Vancouver Island, British Columbia, Canada (Squires and Saul, 2006a) [Area 1]; Gualala Formation, Anchor Bay Member (Elder et al., 1998) [Area 8]; Moreno Formation, Tierra Loma Shale Member, “Quinto Silt,” informal member, and “Garzas Sand” informal member (Squires and Saul, 2003c) [Areas 11, 12]; El Piojo Formation (Squires and Saul, 2006b) [Area 14]; and basal San Francisquito Formation (Squires and Saul, 2006b) [Area 14].

The suprageneric classification of oysters has been in a state of flux during the last two decades. The most current classification scheme, and the one used here, is from Carter et al. (2011). Their scheme will be used for the pending revision of the “Treatise on Invertebrate Paleontology” volume on oysters. Standard morphologic terms are from Stenzel (1971), and those most commonly used here are illustrated in Figures 3–15. Shell-microstructure terms are chiefly from Malchus (1990) and Jaitly et al. (2014).

In compiling the species synonymies, references with accompanying illustrations were used almost exclusively. Nonillustrated references, such as a checklist, were used, but only if museum specimens of the species referred to were seen, thereby allowing for confirmation that the species occurs in beds relatable to the checklist.

To facilitate comparisons, photographs of each studied species were arranged in the following manner: left valve exterior; left valve interior; right valve exterior; and right valve interior. In some cases, anterior or posterior views of a single valve or of conjoined valves are shown, as well as the shell microstructure.

Information about the LACMIP localities is accessible through the website link http://ip.nhm.org/ipdatabase/locality_show. Information about the type localities of the Museum of Paleontology, Berkeley (UCMP), is accessible through the website link <http://ucmpdb.berkeley.edu>. Information about the Canadian localities is incorporated into the appropriate “Stratigraphic Distribution” sections.

ABBREVIATIONS

ANSP

Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania

LACMIP

Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, California

RBCM

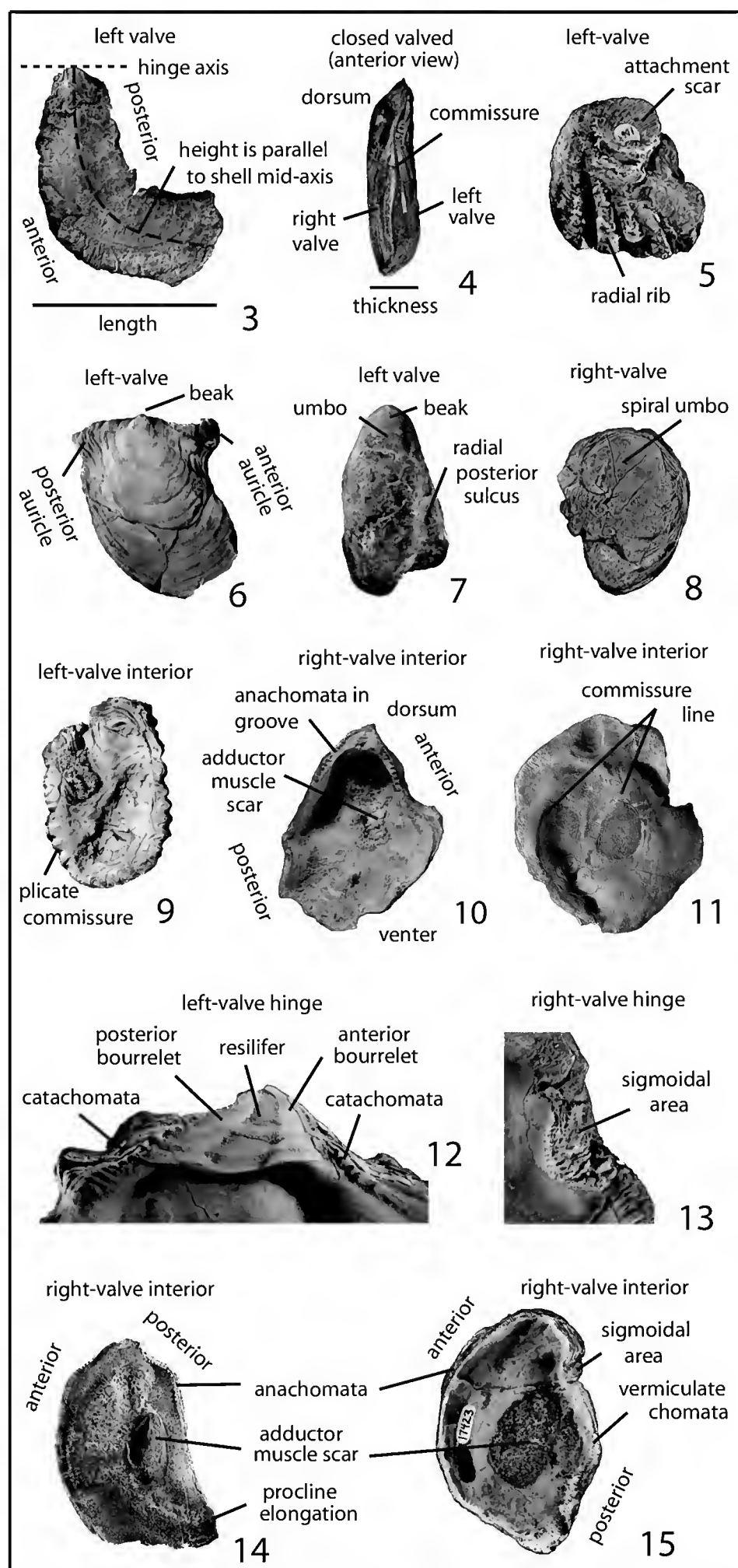
Royal British Columbia Museum, Victoria, Canada

UCMP

University of California Museum of Paleontology, Berkeley, California

VIPM

Vancouver Island Paleontological Museum, Qualicum Beach, British Columbia, Canada



Figures 3–15 Key morphologic terms (after Stenzel, 1971) used in describing oyster shells. **3.** *Curvostrea crescentica*, hypotype LACMIP 14551. **4.** *Curvostrea crescentica*, hypotype LACMIP 14556. **5.** *Costagrya californica*, hypotype LACMIP 14590. **6.** *Pycnodonte* (P.) *malleiformis*, hypotype LACMIP 14618. **7.** *Phygraea inornata*, hypotype LACMIP 14626. **8.** *Amphidonte parasitica*, hypotype LACMIP 14612. **9.** *Rastellum* sp., aff. *R. macropterum*, hypotype LACMIP 14547. **10.** *Acutostrea taxidonta*, hypotype LACMIP 14570. **11.** *Phygraea arida*, paratype LACMIP 14640. **12.** *Acutostrea taxidonta*, hypotype LACMIP 14579. **13.** *Amphidonte parasitica*, hypotype LACMIP 14602. **14.** *Pycnodonte* (P.) *malleiformis*, hypotype LACMIP 14622. **15.** *Amphidonte parasitica*, hypotype LACMIP 14607.

SYSTEMATICS

Order Ostreida Férussac, 1822

Superfamily Ostreoidea Rafinesque, 1815

REMARKS. Fossil oysters are easily recognizable by their distinctive ligamental pit (resiliifer), large adductor muscle scar, and, on certain species, well-developed chomata (denticulations on margins of the valves). Fossil oysters can be abundant, commonly well preserved, and their medium to large size allows for easy detection of the group, either in the field or in museum collections. Generic and specific identification of oysters, on the other hand, can be challenging. As mentioned by Koppa (2015:4–5), the main reasons for this are that they have relatively few unique characters, they likely exhibit significant morphologic variation due to their well-known ecophenotypic plasticity, and they display a distinct propensity for convergence.

Malchus (1990) revised the classification of Mesozoic oysters considerably and restricted *Ostrea* Linnaeus, 1758, and *Lopha* Röding, 1798, to the “Tertiary,” although these genera had been previously regarded as also occurring in older strata. Malchus’ revisions are incorporated here.

Oysters range from Late Triassic to Holocene (Stenzel, 1971:N1051), but they did not become common faunal elements until the Jurassic. Depending on the species, they are indicative of shallow-marine or brackish-marine environments.

Family Arctostreidae Vialov, 1983

Subfamily Arctostreinae Vialov, 1983

Genus *Oscillopha* Malchus, 1990

TYPE SPECIES. *Oscillopha dichotoma* (Bayle, 1849), by original designation; Algeria, Santonian.

AGE AND DISTRIBUTION. Late Cenomanian to Maastrichtian and widespread (Malchus, 1990; Dhondt and Jaillard, 2005). The new species named below is the first record of *Oscillopha* in North America.

REMARKS. Malchus (1990) classified *Oscillopha* in his family Palaeolophidae. According to Carter et al. (2011), paleolophids are now classified in family Arctostreidae Vialov, 1983. *Oscillopha*, a plicate oyster with a large attachment scar, was an epifaunal oyster that abundantly encrusted hard surfaces in shallow seas (middle-shelf environments 20–50 m in depth) (El-Sabbagh, 2008). Its shell microstructure is foliated/homogeneous (Jaitly et al., 2014).

Oscillopha popenoei sp. nov.

Figures 16–25

DIAGNOSIS. Wide, oval, lowly wedge-shaped valves. Large attachment scar. Plicae closely spaced on both valves, 20–25 in number, moderately dichotomous.

DESCRIPTION. Shell size up to height 124 mm (incomplete). Shell oval, rectangular, or slightly crescent shape. Both valves wedge-shaped, with steep plicate wall on anterior margin and much lower plicate wall on posterior margin. Hinge wide, flat, with flat bourrelets and resiliifer indistinguishable. Adductor muscle scar large, ovate, rimmed (especially on anterior side), posterodorsal, and not close to valve margin. Shell microstructure foliated, with lens-shaped layers. **Left valve:** Lowly convex with medium to large attachment area covering up to approximately 75% of valve. Plicae 20–25 in number (two per 7 mm, crest to crest), moderately dichotomous, strong, chevron-shaped, with slightly rounded tops. **Right valve:** Smooth and flat. Umbo reflected posteriorly.

HOLOTYPE. LACMIP 14542, height 92 mm, length 65 mm, LACMIP loc. 25392, Redding Formation, Member VI?, near Clover

Creek Falls on Clover Creek, east of Redding, Shasta County, Northern California.

PARATYPES. LACMIP 14543–14546, all from type locality.

GEOLOGIC AGE. Late Santonian.

GEOGRAPHIC RANGE. East of Redding, Shasta County, Northern California [Area 5].

STRATIGRAPHIC DISTRIBUTION. Redding Formation, Member VI?, near Clover Creek Falls on Clover Creek, east of Redding, Shasta County, Northern California.

REMARKS. Five specimens were examined: three left valves and two right valves. Although there are no complete valves, preservation is good, except for the hinge of the right valve. The hinge is missing on all the left valves.

The sculpture on the new species, especially on the paratype (Fig. 25), is similar to an unnamed variety of *Actinostreon dichotoma* (Bayle, 1849:365–366, pl. 18, figs. 17–18) from Tunisia, north Africa. Pervinqui re (1912:pl. 14, fig. 21) illustrated this variety, which is of Coniacian age. Douvill  (1904:274–275, pl. 37, figs. 1a, 1b) figured *A. dichotoma* of Senonian age from Iran. The Redding Formation species differs from all these illustrations of *A. dichotoma* by having an obvious attachment scar and more closely spaced radial ribs, which are less dichotomous. The Tunisian and Iranian specimens have a posterior auricle that can be small to prominent, but it cannot be determined whether or not a posterior auricle was present on the Redding Formation specimens.

The only other record of *Oscillophra* in the Western Hemisphere is *Oscillophra syphax* (Coquand, 1862), which Dhondt and Jaillard (2005:pl. 1, figs. 6a, 6b) reported from upper Cenomanian strata in northern Peru. The new species differs from this Peruvian species by having half as many radial ribs.

ETYMOLOGY. The new species is named for molluscan paleontologist Willis Parkison (“Parky”) Popenoe, who collected and donated many Late Cretaceous oyster specimens to the University of California Los Angeles invertebrate-fossil collection (now housed at LACMIP) and consistently provided detailed and reliable locality data.

Genus *Rastellum* Faujas-Saint-Fond, 1799

TYPE SPECIES. *Ostrea macroptera* J.D.C. Sowerby, 1825; by subsequent designation (Winkler, 1863); Maastrichtian, Netherlands.

AGE AND DISTRIBUTION. Late Middle Jurassic (Callovian) to Maastrichtian and widespread (except for polar seas) (Stenzel, 1971). The unnamed species described below is the first record of *Rastellum* in the PSNA region.

REMARKS. Some workers (e.g., Stenzel, 1971) have divided *Rastellum* into *Rastellum* (*Rastellum*) and *Rastellum* (*Arctostrea*) Pervinqui re (1910). The morphologic and taxonomic distinctions between *Rastellum* and *Arctostrea* are uncertain, and Stenzel (1971:N1200–N1209) provided in-depth comments about these issues. Malchus et al. (1994) is followed here in treating *Arctostrea* as a hyotespined “form” of *Rastellum* rather than as a subgenus.

Rastellum, a highly plicate oyster, was an epifaunal cementing oyster (Ayoub-Hannaa and F rsich, 2012:125). Its shell microstructure is foliated/homogeneous (Jaitly et al., 2014).

Rastellum sp., aff. *Rastellum macroptera* (J.D.C. Sowerby, 1825)

Figures 9, 26–32

REMARKS. Three specimens were examined, and they are from the middle to upper Turonian Frazier Siltstone Member of the Redding Formation, east of Redding, Shasta County, Northern California [Area 5]. Two of the specimens are from LACMIP loc. 10745 and occur in the same hand specimen. One is a nearly complete left valve (height 75.2

mm) (Figs. 26–30), and the other is a fragment of a left valve (Fig. 32) attached to the larger specimen. The nearly complete left valve, which only shows its very concave interior, is strongly curved (crescentic), very arched with steep parallel flanks, and has a posterior auricle. Numerous angular and prominent radial plicae of uniform size are present along the valve margin and form a zigzag commissure. There are two plicae per centimeter. Most of the hinge of this valve is missing, but along its weathered anterior area there is much foliation of the shell layers. The adductor muscle scar is large, dorsoposterior, and very close to the posterior margin of the valve. The scar is filled with rock matrix and weathers quite differently from the rest of the shell (Fig. 27). On the partial left valve in the hand specimen (Fig. 32), the weathered hinge area consists of foliated shell with no distinct ligamental resilifer/bourrelets preserved, and the adductor muscle scar is crescent-shaped. There are no catachomata. The shell microstructure is foliated/homogeneous.

The third specimen of *Rastellum* sp. is a fragment of the interior of a dorsal surface of a valve from LACMIP loc. 24336 (Fig. 31). It shows the characteristic dorsal keel, as well as remnants of strong plicae.

The three specimens probably represent a new species of *Rastellum*, but it is not named because the specimens are so few and incomplete. They show the most affinity to *Rastellum macroptera* (J.D.C. Sowerby, 1825:105–106, pl. 68, figs. 2, 3), on the basis of the large posterior auricle and on shell size. Stenzel (1971:figs. J138, 1a, 1b) figured Sowerby’s species, which is of Maastrichtian age from the Netherlands. The hinge of the PSNA species, however, is more similar to the hinge illustrated by Cooper (2002:fig. 1A) of the southeastern African *Rastellum allobroensis* (Pictet and Roux, 1853:524–525, pl. 49, figs. 1a–1c) of Albian age.

Family Flemingostreidae Stenzel, 1971

Subfamily Flemingostreini Stenzel, 1971

Tribe Curvostreini Malchus, 1990

Genus *Curvostrea* Vialov, 1936

TYPE SPECIES. *Ostrea rediviva* Coquand, 1869, by original designation; Cenomanian, France.

AGE AND DISTRIBUTION. Early Cenomanian to Maastrichtian and widespread (Seeling and Bengtson, 1999). The species revised here and the new species named below are the first reports of *Curvostrea* in the PSNA region.

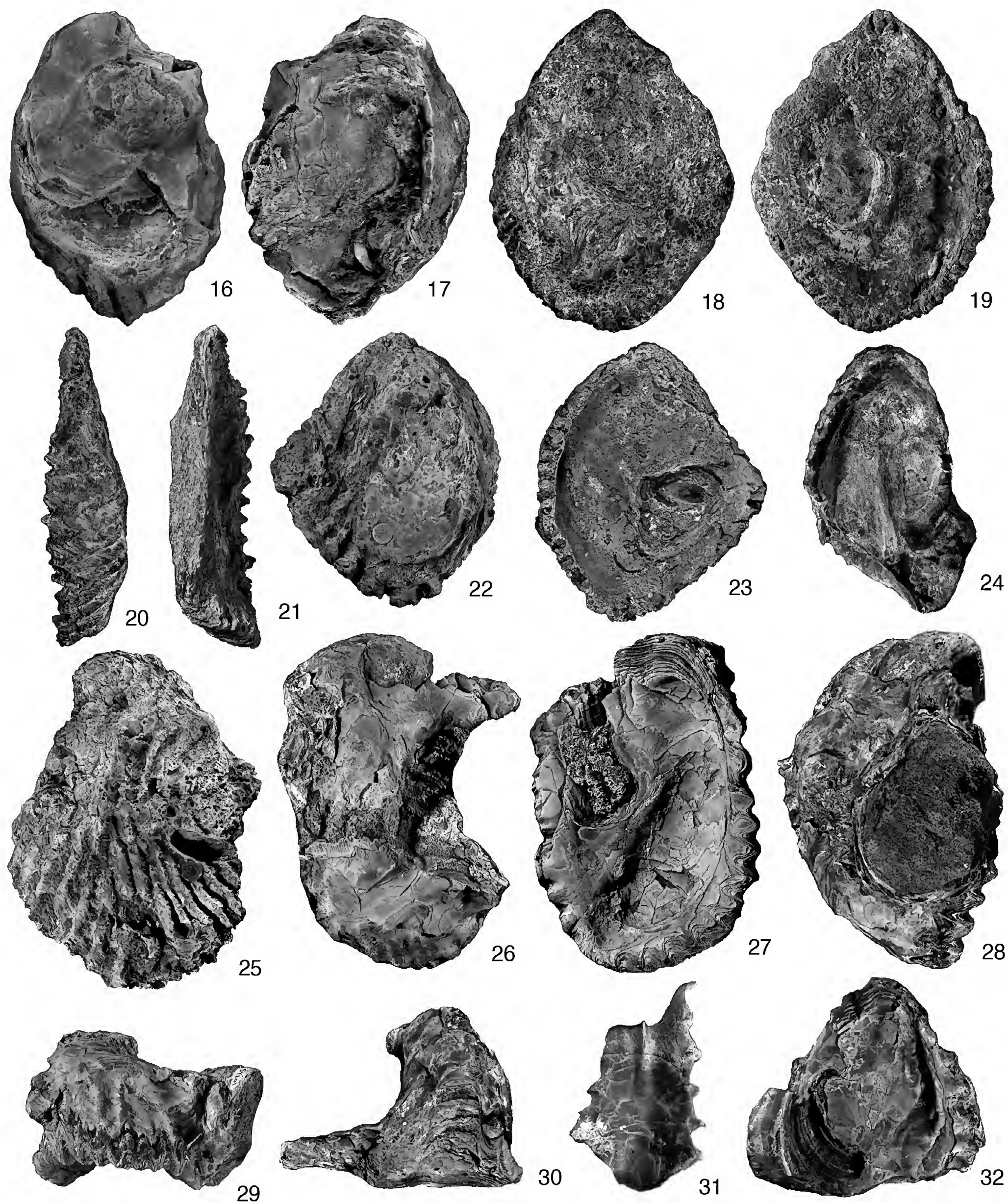
REMARKS. Although Stenzel (1971:N1168) regarded this genus to be of dubious taxonomic value, it has been recognized by numerous workers (e.g., Seeling and Bengtson, 1999:762; Ayoub-Hannaa and F rsich, 2011:89–92, pl. 8, figs. 1–4, text figs. 3.9A, 3.9B). Cooper (1992) reported that *Curvostrea* is a homeomorph of the pycnodontine *Labostrea* Vialov, 1945, of Coniacian to Paleogene age in South Africa. *Curvostrea* differs from *Labostrea* by lacking vesicular shell structure, vermiform chomata, and a commissural shelf with a bordering curb.

Curvostrea was an epifaunal oyster whose cemented left valve is larger and thicker and has a higher preservation potential than its much thinner (lid-like) right valve, which was easily fragmented. This warm-water oyster lived in well-oxygenated, normal-marine conditions associated with a moderately soft substrate and preferred low to intermediate energy levels, with a low degree of environmental stress (Ayoub-Hannaa and F rsich, 2012:111, 125). Its shell microstructure is prismatic/foliated (Malchus, 1990; Jaitly et al., 2014).

Curvostrea crescentica (Packard, 1922) comb. nov.

Figures 3, 4, 33–42

Ostrea crescentica Packard, 1922:420, pl. 26, fig. 3 [not fig. 4 = *Amphidonte parasitica* (Gabb, 1864)]; Sundberg, 1980:844, table 1, unfig.



Figures 16–32 *Oscillopha* and *Rastellum*, Redding Formation [Area 5]. 16–25. *Oscillopha popenoei* sp. nov., LACMIP loc. 25392, Redding Formation, Member VI?. 16–17. Holotype LACMIP 14542, left valve, height 92 mm, $\times 0.6$. 16. Exterior. 17. Interior. 18–21. Paratype LACMIP 14543, left valve, height 124.4 mm, $\times 0.5$. 18.

EMENDED DESCRIPTION. Shell size up to height 68 mm. Shell thin, crescent-shaped, extended posteriorly. Inequivalved. Shell microstructure prismatic/foliated. **Left valve:** Lowly convex and with attachment scar (commonly very small) at dorsal end of valve. Commarginal striae very closely spaced, slightly crenulated or wavy, and forming bands of variable (but narrow) widths. Faint radial bands can be present toward ventral margin. Resilifer small but well defined. Catachomata simple and short but stout posterodorsally, fewer in number anterodorsally. Bourrelets narrow, anterior one slightly wider. Interior of posterior part of left valve can have narrow ridge paralleling shell margin. Adductor muscle scar round, located dorsal of center and near posterior shell margin. **Right valve:** Flattish (lid-like), can be slightly convex posteriorly near hinge. Faint radial striae can be present.

HOLOTYPE. UCMP 12318, height 68 mm, length 60 mm, UCMP loc. 2166, Ladd Formation, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. Ladd Formation, Baker Canyon Member and Holz Shale Member, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922; Sundberg, 1980).

REMARKS. Thirty-two specimens were examined, and many are fragments. Preservation is poor, and exfoliation is common. The holotype, a right valve, has a worn exterior (Fig. 40). All the specimens are in siltstone. Six specimens at LACMIP loc. 8195 in the Baker Canyon Member are conjoined. At this locality, as well as at LACMIP locs. 8169, 10882, and 15738, all within the Baker Canyon Member, *C. crescentica* co-occurs with *Phygraea inornata* (Packard, 1922).

In his caption, Packard (1922:pl. 26, fig. 4) identified specimen UCMP 12319 as belonging to his *Ostrea crescentica*. In his write-up of this species (p. 420), however, he did not even mention this specimen. According to the UCMP records, specimen UCMP 12319 is Packard's paratype of *O. crescentica*, but it is actually a hypotype of *A. parasitica* (Gabb, 1864).

Curvostrea baia sp. nov.

Figures 43–57

DIAGNOSIS. Shell size medium, shape narrow spatulate to subfalcate, posteroventral margins rarely with lateral flanges on both valves; left valve lowly convex, thick, very heavy, thins posteriorly and flattens ventrally, and with no attachment scar; right valve thin, lowly convex, covered with numerous fine, flat radial riblets crossed by commarginal lines, anterior margin beveled; left valve with well-developed, thick, prismatic/foliated microstructure.

DESCRIPTION. Shell size up to height 82 mm. Shape variable, with two morphs: narrow spatulate and subfalcate. Beaks small, poorly developed, ophistograte. Posteroventral margins of both valves rarely with lateral flanges. Adductor muscle scar size medium, elliptical, and located near shell margin just posterior of center of valve. Shell microstructure prismatic/foliated with several, thick, long, and lenticular layers of long (up to 4 mm) perpendicular calcite crystals, separated by

few, very thin nonprismatic layers. **Left valve:** Lowly convex, thin but heavy; valve thinning posteriorly and flattening ventrally. Valve can be slightly wedge shaped, with anterior wall higher than posterior margin. No attachment scar. **Right valve:** Juvenile subtrigonal, umbo inflated, commissure ventrally wavy, resilifer wide, bourrelets indistinct. Anachomata few, short, and extending ventrally from hinge along both margins for less than quarter of total height of valve. Commissural shelf prominent. Adult lowly convex, thin, and with beveled margins; distinct lip present on anterior side. Valve surface covered by many (approximately 15 per millimeter) fine, flat, radial riblets crossing bands of commarginal growth lines that can be raised slightly, thereby creating microscopic cancellate pattern; ribs variable width and can bifurcate; dorsal and medial parts of valve can have few irregular pustulose or lumpy radial ridges. Anachomata only along posterior margin, short and stout on dorsal half of margin but slit-like and more numerous on ventral half of margin. Posteroventral flanges with very weak cancellate lines. Ventral end of valve flattened, with wide border.

HOLOTYPE. LACMIP 14557, height 77 mm, length 36.6 mm, LACMIP loc. 26352, Moreno Formation, "Garzas Sand," Garzas Creek area, west side of San Joaquin Valley, Stanislaus County, Northern California.

PARATYPES. LACMIP 14558–14563. All from type locality or vicinity.

GEOLOGIC RANGE. Late early to early late Maastrichtian.

GEOGRAPHIC RANGE. Garzas Creek area, Stanislaus County, Northern California [Area 11].

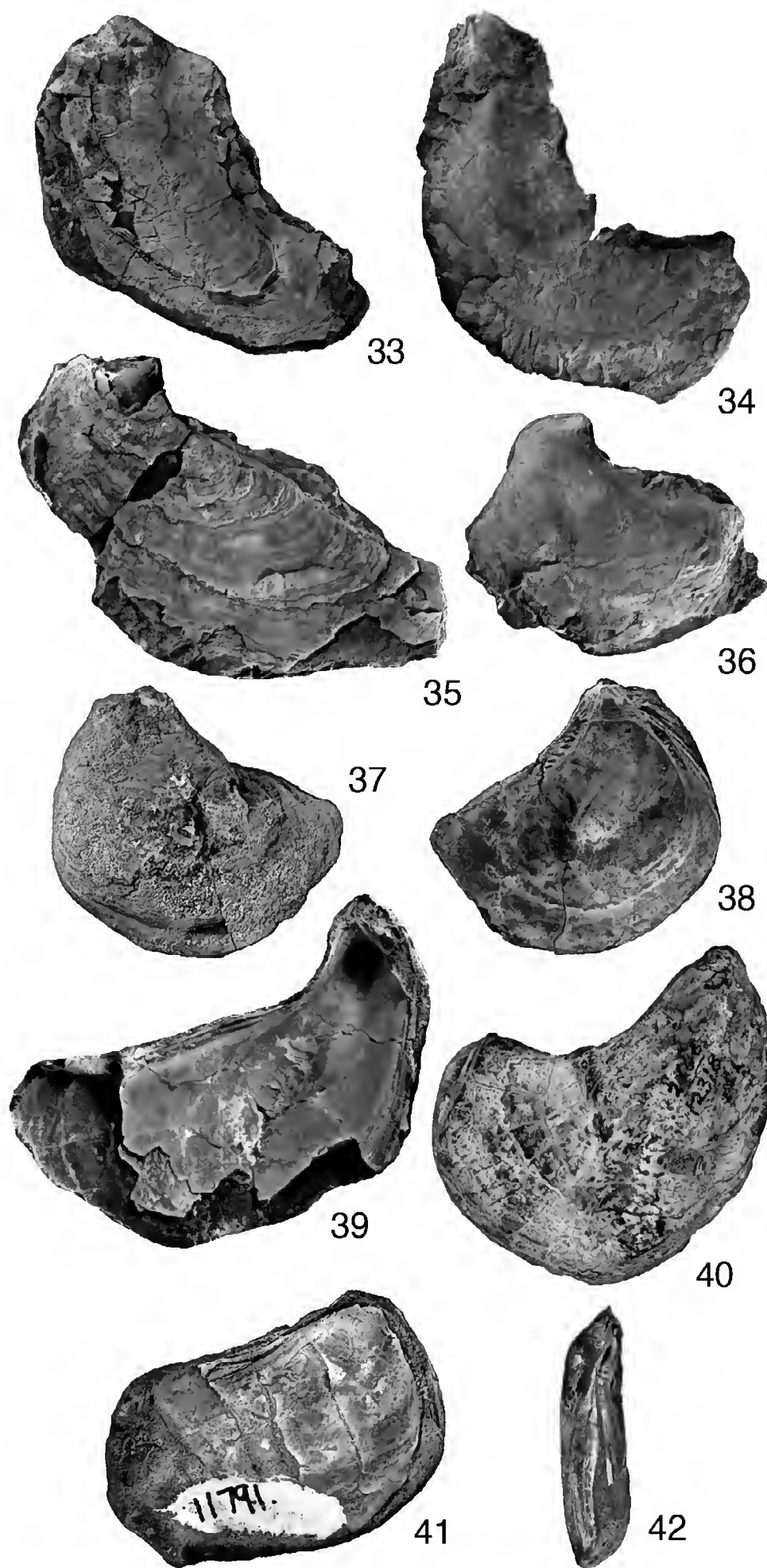
STRATIGRAPHIC DISTRIBUTION. Moreno Formation, "Garzas Sand," Garzas Creek area, west side of San Joaquin Valley, Stanislaus County, Northern California.

REMARKS. Nine specimens were examined: one left valve and eight right valves. Preservation is excellent for the prismatic microstructure of the left valves and also for the exterior sculpture on a few of the right valves. Elsewhere, preservation is moderately poor. Several specimens are tightly conjoined, thereby making it difficult to discern the commissure. A few right valves have eroded remnants of the thick left valve. Some of these same specimens consist of a thin right valve and an associated thick internal cast of the left valve. These casts consist of tightly cemented, smooth, and shiny siltstone that resembles shell material. The two morphs are probably ecophenotypic responses to the environment, but they might be related to growth stage. More specimens are needed to confirm which of these differing suppositions is correct.

The hinge area of the left valve interior (Fig. 44) bears a cast of a wide, sideways U-shaped structure that could possibly be the impression of the bourrelets and resilifer of the right valve hinge. The sideways orientation would indicate that there was a sudden shift in the growth direction of the valves.

The weak radial sculpture of the new species resembles the fine radial sculpture on the right valve of *Ostrea plumosa* Morton (1833:293, 1834:51, pl. 3, fig. 9; Stephenson, 1941:108, pl. 16, figs. 4–6; Akers and Akers, 2002:196, fig. 168, in part), a widespread oyster reportedly of Coniacian to Maastrichtian age in the Gulf and Atlantic coastal plains and in the Colorado-Wyoming-Utah region of the Western Interior of the United States. The new species differs markedly by having a larger

←
Exterior. 19. Interior. 20. Anterior side. 21. Posterior side. 22–23. Paratype LACMIP 14544, left valve, height 87.5 mm, ×0.6. 22. Exterior. 23. Interior. 24. Paratype LACMIP 14545, right valve interior, height 67.5 mm, ×1. 25. Paratype LACMIP 14546, right valve, height 101.7 mm, ×0.6. 26–32. *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825), Redding Formation, Frazier Siltstone Member. 26–30. Hypotype LACMIP 14547, LACMIP loc. 10745, left valve, height 76 mm, ×0.8 (unless otherwise indicated). 26. Exterior. 27. Interior. 28. Posterior side. 29. Edgewise view of venter, height 36.4 mm, ×7. 30. Edgewise view of dorsum, ×0.6. 31. Hypotype LACMIP 14548, LACMIP loc. 24336, left valve interior, height 32 mm, ×1.2. 32. Hypotype LACMIP 14549 (attached to hypotype LACMIP 14547), left valve interior, height 45.3 mm, ×0.9.



Figures 33–42 *Curvostrea crescentica* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16], unless otherwise noted. **33.** Hypotype LACMIP 14550, LACMIP loc. 16860, left valve, height 51 mm, $\times 0.8$. **34.** Hypotype LACMIP 14551, LACMIP loc. 8195, left valve, height 65 mm, $\times 0.8$. **35.** Hypotype LACMIP 14552, LACMIP loc. 8195, left valve, height 58 mm, $\times 0.9$. **36.** Hypotype LACMIP 14553, LACMIP loc. 8195, left valve, height 47 mm, $\times 0.6$. **37–38.** Hypotype LACMIP 14554, LACMIP loc. 21529, Ladd Formation, Holz Shale Member [Area 16], left valve, height 16 mm, $\times 2.1$. **37.** Exterior. **38.** Interior. **39.** Hypotype LACMIP 14555, LACMIP loc. 8195, left valve interior, height 34 mm, $\times 1.5$. **40.** Holotype UCMP 12318, UCMP loc. 2166, height 74 mm, $\times 0.6$. **41–42.** Hypotype LACMIP 14556, LACMIP loc. 11791, conjoined valves, height 28 mm, $\times 1.4$. **41.** Right valve. **42.** Posterior side.

shell (twice as big); more crescentic shape; much flatter, much thicker, and heavier valves; hinge axis straighter; bumps and irregular ridges on the right valve exterior; and less well developed resilifer/bourrelets (not long and narrow). Unlike *C. baia*, the valves of “*O.*” *plumosa* are very thin (nearly eggshell thin) and easily broken.

The new species differs from *Ostrea crescentica* Packard, 1922, by larger size, narrow-spatulate morph, less falcate individuals, thicker and heavier shell, stronger radial sculpture, and much better development of prismatic layers.

The specimens of *C. baia* are in silty, very fine grained sandstone. The flattish to lowly convex, dense left valve, as well as the absence of an attachment scar, are indicative that *C. baia* was a recliner.

ETYMOLOGY. The new species name is derived from *baios* (Greek, meaning “little”), for the fine radial sculpture of the new species.

Subfamily Crassostreinae Scarlato and Starobogatov, 1979

Tribe Crassostreini Scarlato and Starobogatov, 1979

Genus *Acutostrea* Vialov, 1936

TYPE SPECIES. *Ostrea acutirostris* Nilsson, 1827, by original designation; late early Campanian *Belemnelloamax mammilatus* Zone, Sweden (Stenzel, 1971; Christensen, 1997).

AGE AND DISTRIBUTION. Late early Campanian to Oligocene and widespread during the Cretaceous (Cooper, 2002). The species revised here is the first report of Cretaceous *Acutostrea* in the PSNA region. *Acutostrea* is common and widespread in Eocene strata of the PSNA region (Moore, 1987).

REMARKS. *Acutostrea*, which has very variable morphology, was a cementing oyster and an abundant encruster (Wilson and Taylor, 2001:29). Its shell microstructure is prismatic/foliated (Malchus, 1990).

Acutostrea taxidonta (Packard, 1922) comb. nov.

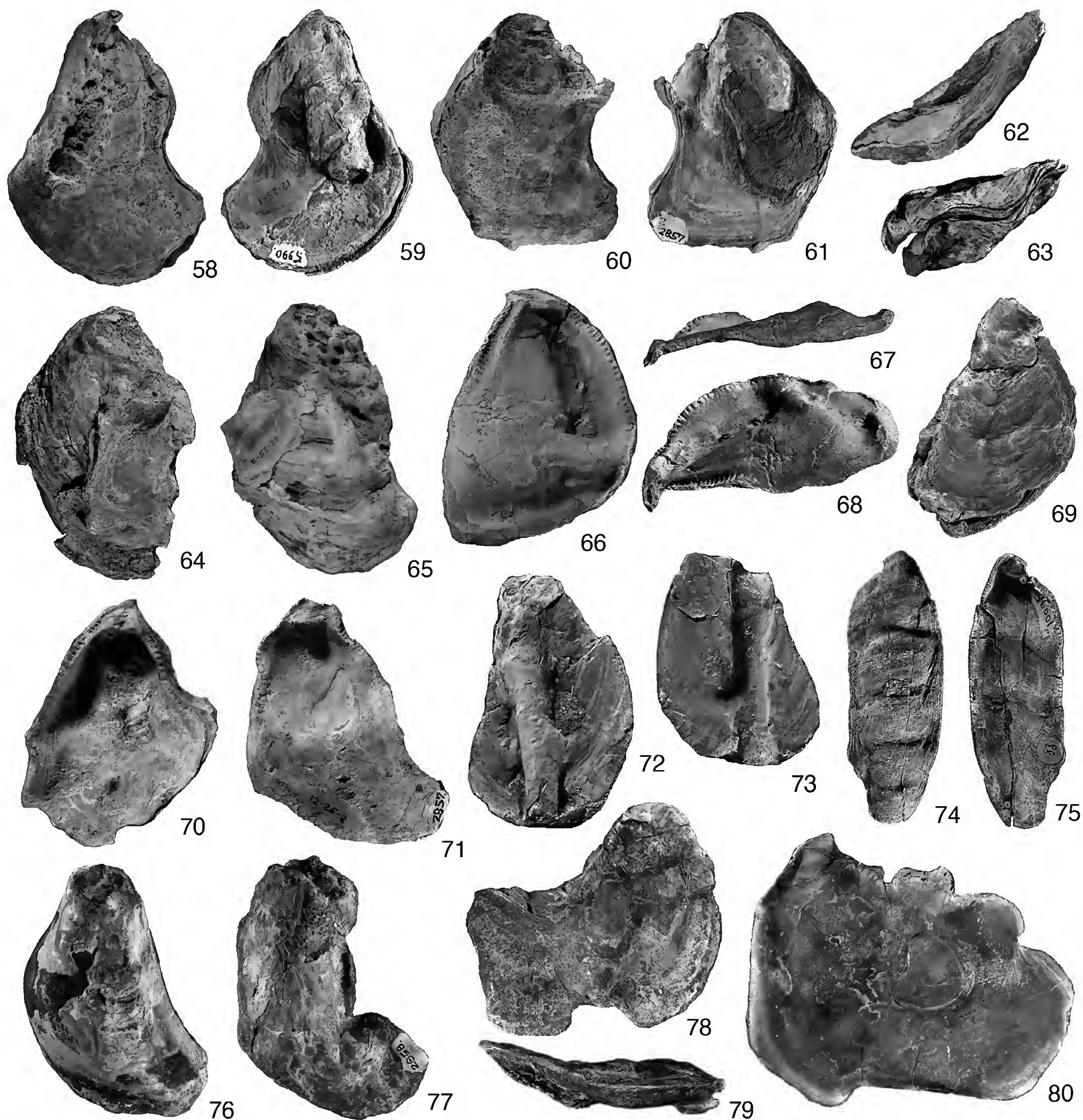
Figures 10, 12, 58–97

Ostrea taxidonta Packard, 1922:420, pl. 26, fig. 2.

EMENDED DESCRIPTION. Shell size up to height 132 mm. Shape highly variable, with five morphs: trigonal, spatulate, suboval, falcate, and irregular. Trigonal and spatulate shapes most common, suboval and falcate shapes uncommon, irregular shapes rare. Trigonal morph mostly small in size but larger ones can be gradational in size and shape with spatulate or falcate morphs. Spatulate morph mostly medium in size but larger ones can be nearly as large as suboval ones (largest morph). Irregular shape small in size, rare, and can fill voids. Ventral half of both valves of all morphs, except irregular, geniculate (bent upward) approximately 40° and also having prominent flexure (sulcus) on medial posterior shell margin. Subequivalved. Resilifer well developed. Adductor muscle scar moderately large, reniform (with pointed end pointing toward hinge), and located near central-posterior margin. Shell microstructure prismatic/foliated. Xenomorphic structure common on left valve and can affect conjoined right valve, as well as interiors of both valves. **Left valve:** Low to moderately low convex. Beak can project beyond right valve beak. Catachomata commonly only on dorsal half of valve, including adjacent to bourrelets. Catachomata straight, those on posterior part of valve longer. Catachomata on larger valves only near hinge, few in number, and generally weak. Valve interior can have irregularities (bumps) near central and ventral regions. Attachment scar on trigonal specimens small to moderate in size, covering beak, and commonly shows outline of foreign matter (commonly long, straight groove with corresponding right valve exterior arched; interiors of valves also reversely affected). Attachment scar wide and large on spatulate specimens; large on suboval specimens, covering



Figures 43–57 *Curvostrea baia* sp. nov., Moreno Formation [Area 11], LACMIP loc. 26352, unless otherwise noted. **43–45.** Paratype LACMIP 14558, left valve, height 83.5 mm, $\times 0.8$. **43.** Exterior. **44.** Interior. **45.** Posterior side, showing predominantly prismatic shell structure. **46.** Paratype LACMIP 14559, right valve, height 32.2 mm, $\times 1.2$. **47–48.** Paratype LACMIP 14560, right valve, height 36 mm, $\times 1.2$. **47.** Exterior of an isolated specimen of three specimens of *A. parasitica* encrusting one another. **48.** Cross-section close-up of thick prismatic shell microstructure, posteroventral part of valve, height 2.5 mm, $\times 8.4$. **49–50.** Paratype LACMIP 14561, conjoined valves, height 43.4 mm, $\times 1$. **49.** Right valve exterior with lateral flanges. **50.** Internal cast of left valve, with remnant of posteroventral shell. **51.** Paratype LACMIP 14562, right valve, height 55.8 mm, $\times 1.1$. **52–56.** Holotype LACMIP 14557, right valve, height 77 mm, $\times 0.9$. **52.** Exterior. **53.** Interior, with remnant of dorsal part of left valve. **54.** Ventral edge view, length 50 mm. **55.** Anterior view. **56.** Posterior view. **57.** Paratype LACMIP 14563, LACMIP loc. 26515, right valve interior, height 74.4 mm, $\times 0.9$.



Figures 58–97 *Acutostrea taxidonta* (Packard, 1922), Rosario Formation [Area 20], unless otherwise noted. **58–59.** Hypotype LACMIP 14564, LACMIP loc. 5990, conjoined valves, height 64.3 mm, $\times 0.7$ **58.** Left valve. **59.** Right valve. **60–62.** Hypotype LACMIP 14565, LACMIP loc. 2857, conjoined valves, height 59.4 mm, $\times 0.6$. **60.** Left valve. **61.** Right valve. **62.** Posterior side. **63.** Hypotype LACMIP 14566, LACMIP loc. 23268, posterior side of conjoined valves, height 48.2 mm, thickness 22 mm, $\times 0.7$. **64.** Hypotype LACMIP 14567, LACMIP loc. 23268, left valve, height, 63.5 mm, $\times 0.7$. **65.** Hypotype LACMIP 14568, LACMIP loc. 2857, left valve, height 78.4 mm, $\times 0.6$. **66–68.** Plastoholotype UCMP 12317, UCMP loc. 2167, Ladd Formation, uppermost Holz Shale Member [Area 16], left valve, height 35 mm, $\times 1.2$. **66.** Interior. **67.** Posterior side. **68.** Oblique view. **69.** Hypotype LACMIP 14569, LACMIP loc. 11975, Tuna Canyon Formation [Area 16], left valve, height 59.1 mm, $\times 0.7$. **70.** Hypotype LACMIP 14570, LACMIP loc. 2857, right valve interior, height 43 mm, $\times 0.9$. **71.** Hypotype LACMIP 14571, LACMIP loc. 2857, attached to hypotype LACMIP 14563, right valve interior, height 64 mm, $\times 0.6$. **72–73.** LACMIP loc. 11957, Tuna Canyon Formation [Area 15], originally conjoined valves. **72.** Hypotype LACMIP 14572, left valve interior (showing xenomorphic bulge), height 38.9 mm, $\times 0.9$. **73.** Hypotype LACMIP 14573, right valve interior with corresponding xenomorphic groove, height 34.6 mm, $\times 1$. **74–75.** Hypotype LACMIP 14574, LACMIP loc. 10095, Ladd Formation, Holz Shale Member [Area 16], right valve, height 57.8 mm, $\times 0.8$. **74.** Exterior, showing xenomorphic replica of external mold of *Turritella* shell. **75.** Interior. **76.** Hypotype LACMIP 14575, LACMIP loc. 23268, left valve, height 65 mm, $\times 0.6$. **77.** Hypotype LACMIP 14576, LACMIP loc. 2858, left valve, height 73 mm, $\times 0.7$. **78–79.** Hypotype LACMIP 14577, LACMIP loc. 11975, Tuna Canyon Formation [Area 15], left valve, length 64 mm, $\times 0.6$. **78.** Interior. **79.** Ventral-edge view. **80.** Hypotype LACMIP 14578, LACMIP loc. 23792, Rosario Formation [Area 19], right valve interior, length 89.1, $\times 0.6$.

most of valve but not on beak; commonly small and covering beak and, rarely, half of valve on falcate specimens; attachment scar not obvious on irregular specimens. **Right valve:** Dorsal half commonly convex but can be flat, posterior half commonly concave to very concave. Exterior surface smooth on nearly all smaller specimens. Commarginal lamellae present on all large specimens but rare on small specimens. Exterior surface of valve can have xenomorphic-caused linear bulge, whereas interior surface can have corresponding hollow area. Valve concave medially. Anachomata short, simple, and present on entire posterior side of valve but becoming weaker and more widely spaced beyond midpoint of valve.

HOLOTYPE. UCMP 12317, height 34.5 mm, length 25 mm, UCMP loc. 2167, Ladd Formation, uppermost Holz Shale Member, Williams Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC RANGE. Middle Campanian to late early to early late Maastrichtian.

GEOGRAPHIC RANGE. North end of Laguna Seca Hills, Merced County, Northern California [Area 12] to Puerto Canoas, Northern Baja California, Mexico [Area 21].

STRATIGRAPHIC DISTRIBUTION. MIDDLE CAMPANIAN: Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, Southern California (Packard, 1922). UPPER MIDDLE CAMPANIAN: Tuna Canyon Formation, South Fork of Garapito Creek, Santa Monica Mountains, Los Angeles County, Southern California (new occurrence). UPPER CAMPANIAN TO POSSIBLY LOWER MAASTRICHTIAN: Point Loma Formation, Carlsbad Research Center, northern San Diego County, Southern California (new occurrence); Rosario Formation (new occurrences) at 1) San Antonio del Mar and 2) "Ammonite Ravine," Santa Catarina and 3) Puerto Canoas, Northern Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation (new occurrence), "Quinto Silt," and "Garzas Sand," north end of Laguna Seca Hills, Merced County, Northern California.

REMARKS. One hundred and nine specimens were examined. Preservation is generally very good. Only a few, including the holotype, are known from the uppermost Holz Shale Member. The holotype (Figs. 66–68), a trigonal morph, is a left valve interior whose exterior is embedded in rock matrix. The ventral margin is not complete, but what is present shows incipient bending (Fig. 67). Specimens of this species are common and generally well preserved in the Rosario Formation, in Northern Baja California, in the San Antonio del Mar, Santa Catarina, and Puerto Canoas areas (Fig. 1). The largest specimens, which are from a single locality (LACMIP loc. 15388) in the Puerto Canoas area, have excellent preservation. Only a single specimen was detected from the Moreno Formation in Northern California.

The trigonal morph of *A. taxidonta* is abundant in siltstone in the Rosario Formation in the Santa Catarina area. The spatulate morph is mainly in very fine to fine-grained sandstones in the Rosario Formation in the San Antonio del Mar area. The suboval morph shape occurs in fine- to medium-grained sandstones in the Rosario Formation in the Punta Canoas area. At LACMIP locs. 22414 and 27263 in the San Antonio del Mar area and at LACMIP loc. 15388 in the Punta Canoas area, both the spatulate and suboval morphs coexist. *Acutostrea taxidonta* co-occurs with *A. parasitica* in the Rosario Formation at LACMIP loc. 27263.

The presence of several morphs of *A. taxidonta* in the Rosario Formation is not incompatible because the basal part of the formation, where specimens of this oyster are abundant, was deposited in a dynamic geologic setting. Miller and Abbott (1989), Lescinsky et al. (1991), and Johnson and Hayes (1993) reported that the basal conglomerate and

sandstone units of the Rosario Formation were pervasive and deposited along a long coastline significantly shaped by subduction tectonism. The advancing (transgressive) sea eroded the margins of the coastline and created rocky shore habitats associated with agitated waters, where both the spatulate and suboval morphs of *A. taxidonta* occur. It is likely that both forms lived in agitated waters, but the suboval forms have a larger attachment surface area because of living in more agitated waters.

Upsection, the basal conglomerate and sandstone units of the Rosario Formation give way to relatively deeper shallow marine units. It is likely that the trigonal morph of *A. taxidonta*, which is found in siltstones in the Santa Catarina area, preferred these slightly deeper and less agitated waters than where the spatulate and suboval morphs lived. For these calmer water specimens, the attachment scar is smaller because of the lower energy water conditions.

Some specimens of the trigonal morph can be noticeably directed posteriorly (Fig. 71), so much so as to grade into the falcate morph (Fig. 77). This gradation occurs at several localities where a sufficient number of specimens (more than 10) were available for comparison (e.g., LACMIP locs. 2857 and 2858 [Rosario Formation, Santa Catarina] and LACMIP loc. 11975 [Tuna Canyon Formation]).

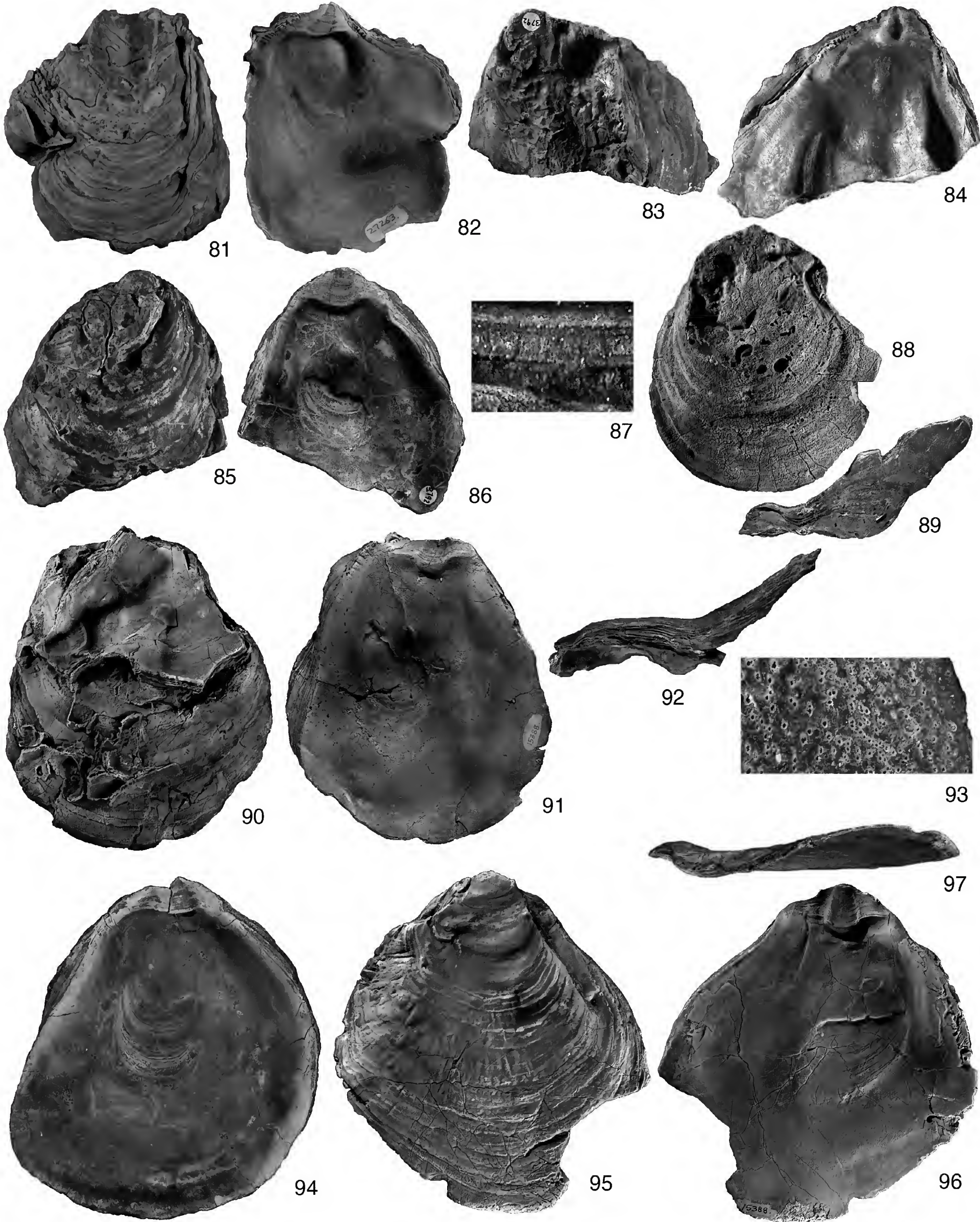
Acutostrea taxidonta is abundant in the Tuna Canyon Formation at LACMIP loc. 11975 in Garapito Canyon, Los Angeles County, Santa Monica Mountains, but preservation is poor because many of these specimens are encased in extremely hard sandstone concretions, and attempts to remove the sandstone matrix result in serious degradation of the shell material. Splitting of the concretions mostly revealed only very poorly preserved interior surfaces of trigonal morphs and a few falcate morphs. On the interior of several of the trigonal left valves is a linear xenomorphic bulge (e.g., Fig. 72). The accompanying right valve (e.g., Fig. 73), which was originally conjoined, has the same linear xenomorphic feature, but it occurs as a groove.

Some conjoined valves of the trigonal morph of *A. taxidonta*, especially from the Santa Catarina area, also show a grooved, linear xenomorphic attachment scar on the exterior surface of the left valve (e.g., Fig. 58) and a corresponding linear bulge on the exterior of the accompanying right valve (Fig. 59).

The irregular morph of *A. taxidonta* is represented by rare individuals attached to narrow gastropod shells. An example (Figs. 74, 75) from the Holz Shale Member of the Ladd Formation is a right valve whose exterior surface (Fig. 74), but not its interior surface (Fig. 75), shows the outline of the whorls and ribs of a *Turritella* gastropod. This oyster grew attached to the inside of an exterior mold of the *Turritella* specimen, thereby indicating a considerable interval of time between the preservation of the *Turritella* specimen and the formation of the oyster specimen.

In terms of its considerable morphologic variability, *A. taxidonta* is very similar to what Cooper (2002:39–43, figs. 6–9) observed for *Acutostrea incurva* (Nilsson, 1827) from upper Campanian to Maastrichtian strata of Europe, Algeria, Russia, and southeast Africa. Cooper (2002:39) stated that the range in morphology of *A. incurva* is "so variable that it almost defies description," and he concluded that this variability is dependent on the size of the attachment area.

Sundberg (1980:845, table 1) listed *Pseudoperma taxidonta* (Packard) as occurring in the Baker Canyon Sandstone Member of Turonian age in the Santa Ana Mountains, Orange County, Southern California. Packard's species, however, is not of Turonian age. In the Santa Ana Mountains, this species is only known from the upper Holz Shale Member of middle Campanian age. The so-called "*Pseudoperma taxidonta*" reported by Sundberg (1980) is most likely the truncated-spatulate morph of *Phygraea inornata* (Packard, 1922), known from the Baker Canyon Sandstone Member.



Genus *Crassostrea* Sacco, 1897

TYPE SPECIES. *Ostrea virginica* (Gmelin, 1791), by original designation; Holocene, Texas.

AGE AND DISTRIBUTION. Middle Jurassic to Holocene and widespread during the Cretaceous (Komatsu et al., 2002). The species revised here is the first Cretaceous report of *Crassostrea* in the PSNA region. *Crassostrea* is represented by several species, some of them of very large size, in Miocene and Pliocene deposits of California and Baja California (Moore, 1987).

REMARKS. This genus is morphologically highly variable, ranging from small size to very large size. Stenzel (1971) reported that *Crassostrea* is characterized by having no chomata. Sohl and Kauffman (1964:7) reported that Mesozoic *Crassostrea* species have chomata, whereas Tertiary species do not. Toulmin (1977) reported, however, Eocene *Crassostrea* with chomata.

Crassostrea, a soft-sediment recliner, is dominant in marginal marine environments but ranges into shallow, nearshore marine situations (Sohl and Owens, 1991:217). Komatsu et al. (2002) reported that this oyster lives today predominantly on muddy bottoms, where a firm basis for attachment is rare. They also reported that individuals of some species are known to have built large colonies to keep their position above the surface of the mud.

Crassostrea brewerii (Gabb, 1864) comb. nov.

Figures 98–113

Ostrea brewerii Gabb, 1864:204, pl. 26, fig. 191.

Odontogryphaea sp. Ludvigsen and Beard, 1994:79–80, fig. 45 (in part), 1997:101–102, fig. 56 (in part).

EMENDED DESCRIPTION. Shell size up to height 190 mm. Shell can be very thick, with left valve up to thickness 44 mm and right valve up to thickness 16.5 mm (not same individual). Shape variable with four morphs: subquadrate, narrow/elongate trigonal, subtrigonal, and rarely crescent. Inequivalved. Elongate posteroventrally. No attachment scar. Resilifer well developed, high and long (up to height 40 mm and length 25 mm), straight or curved (ophistocline). Bourrelets well developed and highly arched, especially ventrally; bourrelets can be equally wide or posterior bourrelet more arched and 2.5 times wider than anterior bourrelet. Adductor muscle scar large, oval with dorsal end “pointed,” and posteroventrally located. Shell microstructure prismatic with numerous thick, long lenticular layers consisting of perpendicular large calcite crystals and separated by thinner, long lenticular layers filled with foliated and recrystallized material. **Left valve:** Convex, ranging from moderately to deeply convex. Valve generally straight-sided; largest specimen with very prominent horizontal, posteroventral bend in ventral region. Posterodorsal area commonly “hump” shaped. Overhang of shell can occur on anterodorsal region. Prominent groove extending along anterior side of valve and noticeable depressed areas just ventral of resilifer and bourrelets, with depression ventral of anterior bourrelets deeper. Chomata rare, near hinge. Large left valves can have chevron-shaped radial costae near ventral margin but not affecting

commissure, except in minor way. **Right valve:** Flattish with upward low deflection on ventral area; valve smooth, moderately thick, with wide ligamental tooth.

HOLOTYPE. UCMP 31447, height 113.7 mm, length 72 mm, UCMP loc. 11381, “Chico Group, Cow Creek” (Stewart, 1930:131), southeast of Redding, Shasta County, Northern California.

GEOLOGIC RANGE. Early Campanian to late middle Campanian.

GEOGRAPHIC RANGE. Nanaimo, Vancouver Island, British Columbia, Canada [Area 2], to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. LOWER CAMPANIAN: Haslam Formation, Upper Quarry on Weigles Road near Brannan Lake, vicinity of Nanaimo, Vancouver Island, British Columbia, Canada (Ludvigsen and Beard, 1994, 1997); Redding Formation, most likely higher than Member VI, possibly South Cow Creek, east of Millville, Shasta County, Northern California (Gabb, 1864); Ladd Formation, Holz Shale Member, Santa Ana Mountains, Orange County, Southern California (new occurrence). UPPER MIDDLE CAMPANIAN: Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County, Southern California (new occurrence).

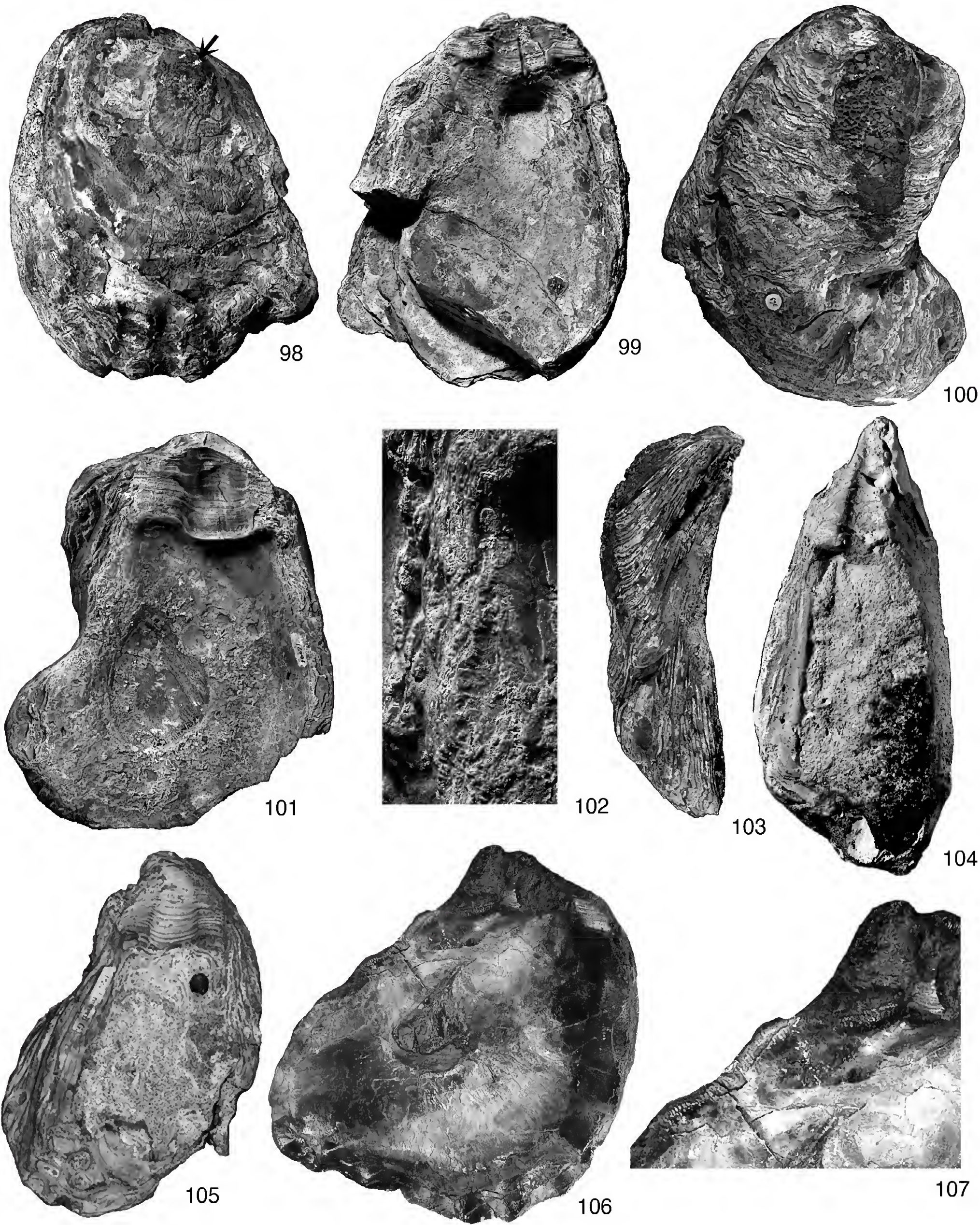
REMARKS. Twelve specimens were examined. Preservation is generally good, but most are large fragments of left valves. The four morphs of this species most likely represent ecophenotypic responses to changes in the environment, but more specimens are needed to confirm this supposition.

All the examined large-size, left-valve specimens from British Columbia and Southern California (Figs. 98, 100, 108) have a moderate to large size (up to diameter 33 mm), conjoined-valved specimen of the mytilid bivalve *Lithophaga* sp., which bored into the posterodorsal “hump” region in or near the umbo. These oyster valves also have small-diameter (up to 4 mm) boreholes, infilled with rock matrix, located elsewhere on them.

Gabb (1864:pl. 26, fig. 191) provided only a sketch of the interior of the left valve of the holotype of *brewerii*, and this sketch shows a projection on the right side of the figure. Stewart (1930:131) reported correctly that this projection is actually another valve, which is in the same hand specimen as the holotype and immediately adjacent to it. Gabb’s holotype (Fig. 105) is shown here with the projection missing, and the immediately adjacent valve is shown separately (Fig. 104). The latter is a slender left valve with a narrow, tapered resilifer, which is a very common feature in *Crassostrea*.

Crassostrea brewerii is the largest and most thick walled Late Cretaceous oyster known from the PSNA region. This species is similar to *Crassostrea cusseta* Sohl and Kauffman (1964:pl.5, figs. 1–4) of Campanian age from the Gulf Coast of the United States, in terms of the following features: heavy, thick shell consisting of thick prismatic layers alternating with much thinner foliated layers, well-developed resilifer and strongly arched bourrelets with subcardinal cavities, rare chomata, and rough exterior surface. *Crassostrea brewerii* differs by being smaller (*C. cusseta* has an average shell height of 377 mm) and in having

Figures 81–97 *Acutostrea taxidonta* (Packard, 1922), Rosario Formation [Area 19], unless otherwise noted. **81–82.** Hypotype LACMIP 14579, LACMIP loc. 27263, left valve, height 82 mm, $\times 0.5$. **81.** Exterior. **82.** Interior. **83–84.** Hypotype LACMIP 14580, LACMIP loc. 23792, partial left valve, height 68 mm, $\times 0.5$. **83.** Exterior. **84.** Interior. **85–87.** Hypotype LACMIP 14581, LACMIP loc. 23792, partial left valve, height 80 mm, $\times 0.5$. **85.** Exterior. **86.** Interior. **87.** Cross section of prismatic/foliated shell microstructure, near hinge on anterodorsal margin of valve, width 4 mm, $\times 10$. **88–89.** Hypotype LACMIP 14582, LACMIP loc. 15388, Rosario Formation [Area 21], left valve, height 104.3 mm, $\times 0.5$. **88.** Exterior. **89.** Posterior side. **90–93.** Hypotype LACMIP 14583, LACMIP loc. 15388, Rosario Formation [Area 21], left valve, height 133 mm, $\times 0.4$. **90.** Exterior. **91.** Interior. **92.** Posterior side. **93.** Close-up of pervasive microborings on interior of valve, near medial-anterior margin, height 2 mm, $\times 10$. **94.** Hypotype LACMIP 14584, LACMIP loc. 15388, Rosario Formation [Area 21], left valve interior, height 131.5 mm, $\times 0.5$. **95–97.** Hypotype LACMIP 14585, LACMIP loc. 15388, Rosario Formation [Area 21], right valve, height 129.6 mm, $\times 0.5$. **95.** Exterior. **96.** Interior. **97.** Posterior side.



wide-spatulate rather than narrow-elongate shape, a shorter bend ventrally in the shell, and a better developed adductor muscle scar.

Family Gryphaeidae Vialov, 1936

Subfamily Exogyrinae Vialov, 1936

Genus *Costagyra* Vialov, 1936

TYPE SPECIES. *Exogyra olisipoensis* Sharpe, 1850, by original designation; Cenomanian to Turonian, Portugal, Jordan, and Utah (Reeside, 1929; Malchus, 1990; Agrabawi, 1993).

AGE AND DISTRIBUTION. Early Cenomanian to Maastrichtian and widespread (except in polar seas) (Reeside, 1929; Stenzel, 1971). The species revised here and the new species named below are the first reports of *Costagyra* in the PSNA region.

REMARKS. Early workers (e.g., Reeside, 1929; Stenzel, 1971) used *Costagyra* as a subgenus of *Exogyra* Say, 1820, although the radial ribs on *Costagyra* are fewer, stronger, and more widely spaced. Most modern workers (e.g., Dhondt et al., 1999; Dhondt and Jaillard, 2005; Ayoub-Hannaa and Fürsich, 2011; Hannaa, 2011) elevated *Costagyra* to the genus level, and their practice is followed here.

Costagyra juveniles were cemented to secondary hard substrate, whereas adults were adapted to a free, reclining mode of life on soft sediment. The thick shells of some species served to increase stabilization on the soft sediment and also helped to protect against predators (Ayoub-Hannaa and Fürsich, 2011). Variations in shell thickness and ornament of *Costagyra* were possibly related to water energy (Seeling and Bengtson, 1999:758). Its shell microstructure is predominantly prismatic, with some foliated layers (Jaitly et al., 2014).

Costagyra californica (Packard, 1922) comb. nov.

Figures 5, 114–120

Exogyra californica Packard, 1922:421, pl. 27, fig. 5.

EMENDED DESCRIPTION. Shell size up to height 55 mm. Shape rectangular to subfalcate. Inequivalved. Umbonal region tightly spirally coiled posteriorly. Shell microstructure predominantly prismatic with much thinner foliated layers. **Left valve:** Convex with medial axis coincident with broad, bumpy keel extending posteriorly from umbo to venter; keel can be continuous or with broad sulcus on medial part of valve. Posterior side of valve bearing nine to 10 ribs (can be dichotomous) which extend from umbo to venter and widen toward venter; radial ribs narrow to moderately wide and can be nearly hyote-like near venter; interspaces wide and concave. Attachment area present on small specimens. **Right valve:** Flat to slightly concave (near hinge) and smoothish, with overlapping spirally arranged growth lamellae. Radial ribs short (approximately eight) along anterior side of first whorl of spiraling umbo, with ribs becoming wider, more widely spaced, and less prominent with increasing size of whorl. Resilifer groove narrows posteriorly and can be nearly filled with shell deposit. Anterior bourrelet thin, coincident with sharp anterior edge of shell, and bearing many short anachomata. Posterior bourrelet forms short projecting ridge

adjacent to concavity just ventral of hinge line. Adductor muscle scar large, reniform, and just posterior of central part of valve.

HOLOTYPE. UCMP 12320, UCMP loc. 2143, height 57 mm, length 60 mm, Ladd Formation, Baker Canyon Member, east side Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. ?Ono area, Shasta County, Northern California [Area 6] to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. QUESTIONABLY UPPER CENOMANIAN: Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County, Northern California (new occurrence). TURONIAN: Ladd Formation, Baker Canyon Member and Holz Shale Member, east side Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922).

REMARKS. Sixteen specimens were examined. Preservation is moderately poor, and the radial ribs are very faint on most specimens because of weathering, including the holotype (Fig. 114). Many of the specimens of this species are internal casts, including a questionable occurrence of this species from LACMIP loc. 10878 in the Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County, Northern California. *Costagyra californica* co-occurs with *P. inornata* at LACMIP locs. 10887 (Baker Canyon Member) and 15894 (Holz Shale Member). A small left valve (Fig. 115) of *C. californica* from LACMIP loc. 8198 (Baker Canyon Member) shows a moderately large attachment scar.

Costagyra garza sp. nov.

Figures 121–127

Exogyra sp. Elder and Miller, 1993:table 3.

DIAGNOSIS. Shell size large, *Costagyra* with keeled left valve bearing 12 to 13 radial ribs.

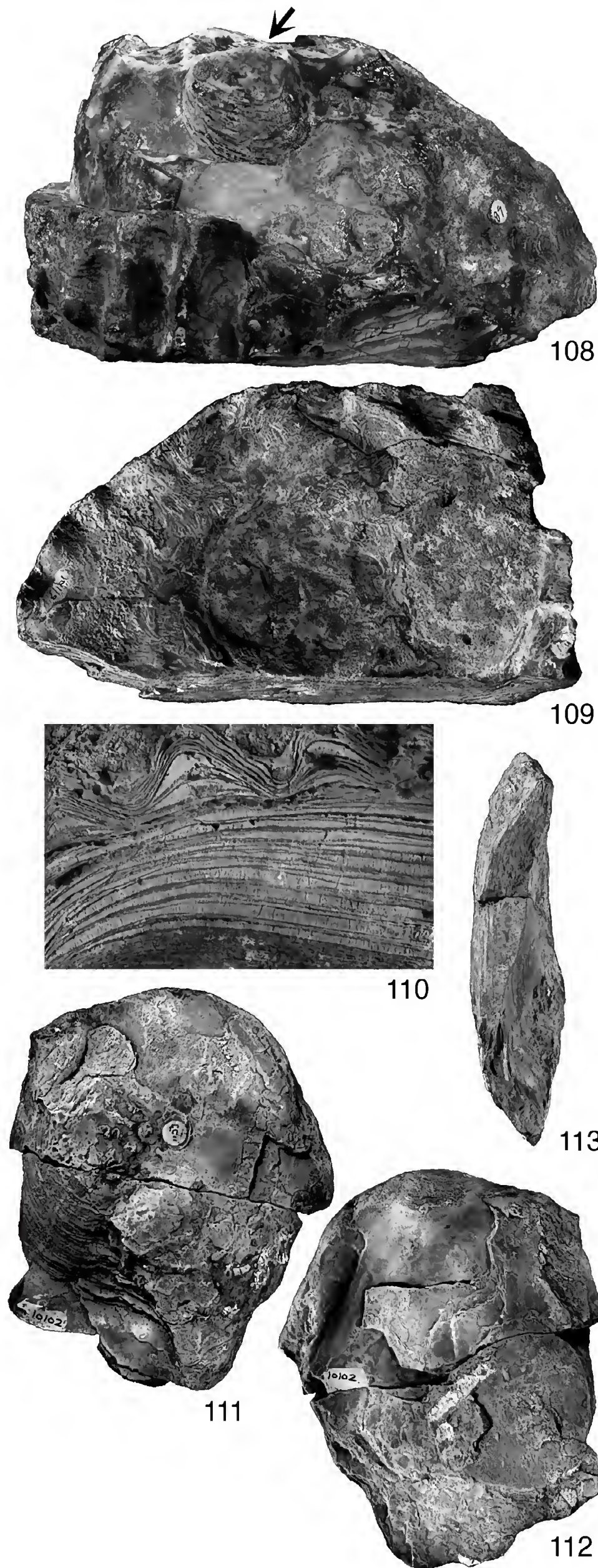
DESCRIPTION. Shell size up to height 100 mm. Shape subfalcate to falcate. Very inequivalved, beaks spirally coiled. Shell microstructure predominately prismatic with some much thinner foliated layers. **Left valve:** Inflated greatly. Radial ribs 12 to 13, wide, can be dichotomous, and with moderately wide interspaces; ribs extend to umbo where partly covered by thin shell with rugose growth lines; ribs become wider ventrally and have development of some hyote-like raised areas; ribs obsolete on some large specimens. **Right valve:** Smooth, lid-like, thin; ventral half sunken, whereas dorsal half turns upward. Adductor muscle scar central.

HOLOTYPE. LACMIP 14594, height 92.8 mm, length 84.4 mm, LACMIP loc. 26517, Moreno Formation, “Garzas Sand,” Garzas Creek, western side San Joaquin Valley, Stanislaus County, Northern California.

PARATYPES. LACMIP 14595–14597. All from vicinity of the holotype.

GEOLOGIC RANGE. Late early to early late Maastrichtian.

←
Figures 98–107 *Crassostrea brewerii* (Gabb, 1864), Ladd Formation, Holz Shale Member [Area 16], unless otherwise noted. **98–99.** Hypotype LACMIP 14586, LACMIP loc. 24190 left valve, height 133.3 mm, $\times 0.5$. **98.** Exterior with boring bivalve *Lithophaga* sp. on posterodorsal umbo region (denoted by arrow). **99.** Interior. **100–103.** Hypotype LACMIP 14587, LACMIP loc. 10091, left valve, height 142.6 mm, $\times 0.5$, unless otherwise noted. **100.** Exterior with boring bivalve *Lithophaga* sp. and encrusting annelid? tubes on posterodorsal umbo region. **101.** Interior. **102.** Close-up, ventral of hinge, of posterior shell margin bearing catachomata, height 40 mm, $\times 1.7$. **103.** Posterior view. **104.** Plaster replica of left valve interior of specimen, height 100 mm, $\times 0.8$, attached to anterior side of holotype of *C. brewerii*. **105.** Holotype UCMP 31447, UCMP loc. IP 11381, “Chico Group, Cow Creek” [Area 5], left valve interior, height 117 mm, $\times 0.6$. **106–107.** Hypotype VIPM 017, Haslam Formation [Area 2], left valve interior. **106.** Height 140 mm, $\times 0.5$. **107.** Close-up, ventral of hinge, of posterior shell margin bearing catachomata, height 23 mm, $\times 2$.



GEOGRAPHIC RANGE. Garzas Creek area, Stanislaus County, Northern California [Area 11].

STRATIGRAPHIC DISTRIBUTION. Moreno Formation, "Garzas Sand," Garzas Creek, west side San Joaquin Valley, Stanislaus County, Northern California.

REMARKS. Seven specimens were examined. Preservation is moderately good. Two of the specimens are conjoined. *Costagrya garza* differs from *C. californica* by having a much larger size, nonrectangular shape, and more radial ribs. The new species is very similar to *Costagrya olisipoensis* illustrated by Malchus (1990:pl. 10, figs. 6a, 6b) and by Aqrabawi (1993:pl. 4, figs. 3–5, pl. 5, figs. 1, 2). The new species differs by having no hyote spines, a less prominent umbo (i.e., wide and projected), and no ribs on the right valve.

Elder and Miller (1993:table 3) reported *Exogyra* sp., of middle or approximately middle Maastrichtian age, from the Garzas Creek area, Stanislaus County, Northern California. The specimens they examined are the same ones examined for this present report: LACMIP locs. 6357 [now 26357], 6358 [now 26358], 10660, and 6517 [now 26517].

ETYMOLOGY. The new species is named for the "Garzas Sand."

Tribe Amphidonteini Vialov, 1983

Genus *Amphidonte* Fischer de Waldheim, 1829

TYPE SPECIES. *Amphidonte humboldtii* Fischer de Waldheim, 1829, by subsequent designation (Fischer, 1886); Late Cretaceous (Cenomanian), Russia.

AGE AND DISTRIBUTION. Early Cretaceous to late Maastrichtian and widespread (Aqrabawi, 1993). The species revised here is the first report of *Amphidonte* in Northern Baja California, Mexico.

REMARKS. Stenzel (1971) did not recognize any subgenera of *Amphidonte*, whereas many subsequent workers (e.g., Elder, 1991; Aqrabawi, 1993; Malchus et al., 1994; Seeling and Bengtson, 1999) recognized *Ceratostreon* Bayle, 1878, as a subgenus of *Amphidonte*.

Lazo (2007) reported *Amphidonte* to be a cementing, epifaunal bivalve, and LaBarbera (1981) reported it to be an epifaunal recliner, generally on soft sediment. Its shell microstructure is compact foliated with lens-shaped layers (Malchus, 1990).

Amphidonte parasitica (Gabb, 1864)

Figures 8, 13, 15, 128–155

Exogyra parasitica Gabb, 1864:205, pl. 26, figs. 192, 192a, 192b; pl. 31, figs. 273, 273a; Whiteaves, 1879:175, 1903:401, 409; White 1884:306, pl. 55, figs. 3, 4 (after Gabb); Stewart, 1930:132, pl. 1, fig. 1.

Ostrea washingtoni Coquand, 1869:63–64, pl. 33, figs. 5–9 (after Gabb); unnecessary new name for *Exogyra parasitica* Gabb. Not *Ostrea parasitica* Lindroth, 1788:17; not *Ostrea parasitica* Gmelin, 1791:3336.

Ostrea crescentica Packard, 1922:pl. 26, fig. 4 [not *Ostrea crescentica* Packard, 1922:420, pl. 26, fig. 3].

Figures 108–113 *Crassostrea brewerii* (Gabb, 1864), Williams Formation, Pleasants Sandstone Member [Area 16], unless otherwise noted. **108–110.** Hypotype LACMIP 14588, LACMIP loc. 10119, partial left valve, height 100 mm, $\times 0.5$. **108.** Exterior, with partial specimen of boring bivalve *Lithophaga* sp. (denoted by arrow). **109.** Interior. **110.** Cross-section showing prismatic/foliated shell microstructure, middle part of ventral edge of valve, height 31 mm, $\times 1.1$. **111–113.** Hypotype LACMIP 14589, LACMIP loc. 10102, Ladd Formation, Holz Shale Member [Area 16], right valve, height 107.6 mm, $\times 0.5$. **111.** Exterior. **112.** Interior. **113.** Posterior view.

Amphidonte (Amphidonte) parasitica (Gabb). Elder, 1991:E11, pl. 4, figs. 9, 17–23.

Amphidonte sp. cf. *A. parasitica* (Gabb, 1864). Elder et al., 1998:pl. 1, fig. 14.

Amphidonte parasitica (Gabb). Kennedy et al., 2000:16.

?*Amphidonte (Amphidonte) parasitica* (Gabb). Elder, 1991:pl. 3, figs. 6, 10.

EMENDED DESCRIPTION. Shell size normally up to height 80 mm, rarely up to 100 mm. Shape variable with three morphs: auriform (ear-like), wedge, and short tube, listed in decreasing order of abundance. Auriform morph with shell height approximately 17–70 mm, wedge morph shell height approximately 53–100 mm, and short-tube morph shell height 20–60 mm. Auriform morph gradational in shape with wedge morph and, to lesser degree, with short-tube morph. Valve exteriors smooth, with only growth lamellae (if any). Adductor muscle scar size medium to large; scar shape oval on all morphs, and either central or off-center, near posterior wall. Umbo opisthogyral to various degrees. Hinge area commonly strongly coiled but can be poorly developed and wide. Resilifer not prominent on most specimens. Sigmoidal sinus (notch) can consist of infolded area where chomata bend abruptly in half-circle fashion, affecting both valves near posterior bourrelet, causing margin of the sinus to be wrinkled and forming small depression in left valve and corresponding slight bulge in right valve. Sigmoidal sinus can be “closed up” on some specimens. Ligamental area can remain obscure to weak or moderately strong. Chomata small, numerous and cover both interior margins of each valve or can be obscure. Shell microstructure foliated, with lens-shaped layers. **Left valve:** Attachment surface flat or slightly concave and commonly smoothish on all morphs. Smallest specimens (shell height 17 mm) crescent-shaped with wide umbo, hinge spirally coiled, and resilifer and sigmoidal sinus not obvious or poorly developed. Early adult to mature adult auriform-morph individuals (shell height normally 35–43 mm, but uncommonly can be up to 70 mm) with generally flattish valve, anterior wall slightly to moderately elevated with respect to posterior wall, umbo broad, hinge spirally coiled, resilifer obscure, sigmoidal sinus well developed, and chomata well developed. At approximate shell height 35 mm, auriform-morph anterior wall can become gradationally more elevated (increasing from 21 to 32 mm high, rarely up to 50 mm high), and also nearly vertical to vertical; posterior wall much lower (increasing from 5 to 13 mm high) and much thinner. At approximate shell height 50–58 mm, and continuing to shell height 80 mm, anterior wall elevated enough and thick enough to form wedge morphs. Distinction between specimens intermediate in shape between auriform and wedge morphs is arbitrary because change in the height of anterior wall relative to the posterior wall is gradational. Wedge morph has left valve sloping approximately 30° from highest point toward posterior margin; in addition, umbo spirals posterior and begins to “close up,” as does sigmoidal sinus. Anterior wall normally smooth but can be broadly lumpy, with broad sulcus between two lumps. Short-tube morph only known from left valves, anterior wall thin (up to 14 mm high) and more elevated than posterior wall (up to 5 mm high), thereby producing overall partial wedge shape (depending on view). Short-tube morph flat bottomed (well cemented to hardground), resilifer small, sigmoidal sinus area generally obscured, and adductor muscle scar circular. **Right valve:** Auriform immature valves (less than shell height 20 mm) known only from right valves, flattish to lowly convex, with ligamental area very poorly developed (barely discernible), small indentation to accommodate spiraling of beak, and sigmoidal sinus absent. Auriform adult right valves flat (lid-like), smooth, thin but with some thickening anteriorly, especially on dorsoanterior region. As umbo spirals posterior, ligamental area can narrow and begin to “close up,” as does sigmoidal sinus

(especially on wedge morphs). Ligamental area rarely very wide and obscure. On some auriform specimens (shell height 70 mm), right valve countersunk into groove of corresponding left valve, with numerous, short, and closely spaced anachomata on right valve margin meshing with chomata on overlapping left valve.

LECTOTYPE. ANSP 4429 (designated here), height 39.2 mm, length 26.3 mm, Chico Formation, Granite Bay [= Texas Flat], Amador County, Northern California. Gabb (1864) did not select a holotype of *E. parasitica*, nor did Stewart (1930), who re-examined Gabb’s type specimens. Stewart (1930) suggested that ANSP 4429 might be a suitable lectotype but did not designate it as such. Specimen ANSP 4429 is designated here as the lectotype.

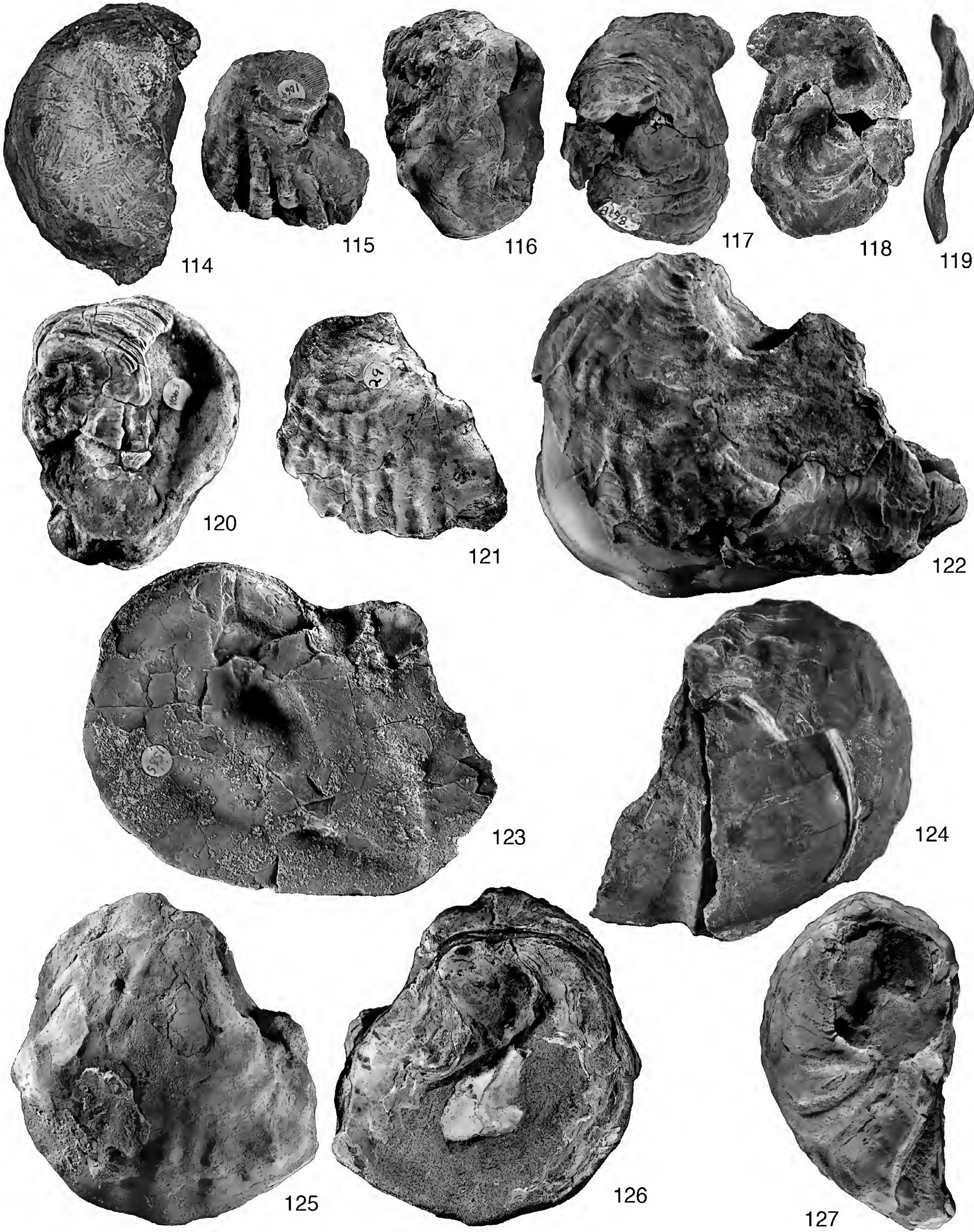
GEOLOGIC RANGE. Early Campanian to latest Maastrichtian.

GEOGRAPHIC RANGE. Denman Island and Hornby Island off east coast of Vancouver Island, British Columbia, Canada [Area 1], to San Antonio del Mar, Northern Baja California, Mexico [Area 19].

STRATIGRAPHIC DISTRIBUTION. LOWER CAMPANIAN: Chico Formation, Pentz, Butte County, Northern California (Eric Göhre, personal communication, 2002); Chico Formation, Granite Bay [= Texas Flat], Amador County, Northern California (Gabb, 1864). UPPER MIDDLE CAMPANIAN [*Metaplaenticeras* cf. *pacificum* ammonite zone (see Ward et al., 2015:fig. 7)]: Upper Cedar District Formation, “White House” site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada (new occurrence); unnamed formation, Loma Prieta area, Santa Cruz Mountains, Santa Clara County, Northern California (Elder, 1991); Williams Formation, Pleasants Sandstone Member, Bee Canyon, Santa Ana Mountains, Orange County, Southern California (new occurrence). UPPER CAMPANIAN/LOWER MAASTRICHTIAN: Northumberland Formation, Collishaw Point, “shark tooth zone,” Hornby Island, off east coast of Vancouver Island, British Columbia (new occurrence); Gualala Formation, Anchor Bay Member, west of Anchor Bay, Mendocino County, Northern California (Elder et al., 1998); an unnamed fault-bounded stratigraphic unit, Loma Prieta, Santa Cruz Mountains, Santa Clara County, Northern California (Elder, 1991); basal Point Loma Formation, Palmer Way, Carlsbad, San Diego County, Southern California (Kennedy et al. 2000); Point Loma Formation, La Jolla, San Diego County, Southern California (new occurrence); Rosario Formation (new occurrence), Punta San Jose and San Antonio Del Mar, Northern Baja California, Mexico. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Tierra Loma Shale, north end of Laguna Seca Hills, Merced County, Northern California (new occurrence). UPPERMOST MAASTRICHTIAN: El Piojo Formation, Cantinas Creek and Dip Creek, Lake Nacimiento, San Luis Obispo County, Northern California (Saul, 1986a); San Francisquito Formation, Warm Springs Mountain, Los Angeles County, Southern California (Kirby, 1991).

REMARKS. Eighty-five specimens were examined. Preservation is best in the Point Loma Formation near Carlsbad, San Diego County; the Rosario Formation at San Antonio del Mar, Baja California, Mexico; and the Cedar District Formation on western Denman Island, British Columbia, Canada. Elsewhere, preservation is generally good. The short-tube morph (e.g., Figs. 141, 142) is only found in the Point Loma Formation in the Carlsbad area and in the upper Cedar District Formation on western Denman Island. The lectotype of *A. parasitica* is an early adult-auriform morph, and two views of a plaster cast of the lectotype are shown in Figures 131 and 132.

Elder (1991:E11, unfig.) reported the largest specimen of *A. parasitica* as having a shell height of 100 mm. It is from an unnamed fault-bounded stratigraphic rock unit near Loma Prieta [Area 11]. Elder (1991:pl. 4, figs. 9, 17–23) illustrated several morphs of *A. parasitica* found in this rock unit and referred to them as “typical” and “ovate”



[both same as auriform here], “ovate with carinate umbilical ridge” [same as short tube here], and “elongate.” Based on the low profile, robust shell, and large attachment surface of many of the oysters, they were adapted to a nearshore, high-energy environment. In the rock unit near Point Loma, they subsequently underwent transport downslope by turbidity currents and into deeper waters, where they accumulated as oyster coquinas (Elder, 1991).

A growth stage series of the auriform morph, ranging in height from 20 to 70.6 mm (Figs. 128–145), is best represented at LACMIP loc. 3966 in the Point Loma Formation, at Madonna Hill in the Carlsbad area, San Diego County [Area 17]. At this locality, the majority of the specimens represent the auriform morph, a few somewhat resemble the wedge morph, and a few are the short-tube morph. At other localities in the immediate vicinity, specimens are represented by the auriform and wedge morphs or by the auriform and those that resemble the wedge morphs. At nearby LACMIP loc. 17423, a large auriform morph (shell height 70 mm) with conjoined valves (Figs. 143–145) was collected.

The presence of growth stages and conjoined valves are strongly indicative that *A. parasitica* auriform morphs found in sandstones of the Point Loma Formation, Carlsbad area, San Diego County, are in situ or nearly so. Kennedy et al. (2000) interpreted the depositional environment at the Palmer Way localities in the Point Loma Formation to have been an intertidal? to a very shallow, nearshore marine, rocky bottom habitat. The common co-occurrence of auriform and the sturdier looking wedge morphs is suggestive that microenvironments (e.g., possibly protected habitats versus more exposed habitats, respectively) played a role in determining the morph shape. Detailed sedimentologic and paleoenvironmental studies, which might help to understand the variability of morph shapes found at these Carlsbad localities, cannot be made because the specimens were collected from temporary exposures of medium-grained (on average) sandstone at several localities (e.g., LACMIP 3966, 17423), just a few meters stratigraphically above a basal conglomerate. All these beds were destroyed in subsequent development.

In the Rosario Formation at LACMIP loc. 27263, in the San Antonio del Mar area, Baja California, Mexico [Area 19], both the auriform and wedge morphs are present, but the auriform morph (Fig. 146) is a minor component compared with the wedge morph (Figs. 147, 150). The specimens are robust and heavy, mostly free of sandstone matrix, and dark gray. Many of the specimens have large prominent “holes” (openings caused by dissolution) coincident with former position of the adductor muscle scar (Figs. 146, 147). One hand specimen (Fig. 147) contains three large specimens (height 60–82 mm) of *A. parasitica*, which solidly encrust one another. The specimen shown in Figure 147 is an auriform morph isolated from the hand specimen, whereas the other two specimens are more wedge shaped. Also at locality 27263, a left valve of a wedge morph of *A. parasitica* (Fig. 150) is totally cemented to a right valve of a trigonal morph of *A. taxidonta*. Sedimentologic and paleoenvironmental analyses are so far lacking for rocks at this locality.

Only the wedge morph (e.g., Figs. 148, 149, 151, 152) is known from LACMIP loc. 22415 in the Williams Formation, Pleasants Sandstone Member, Santa Ana Mountains, Orange County [Area 16]; specimens are not common. The left valves are thick and robust (i.e., sturdy looking). These Bee Canyon exposures are slightly younger than the Pleasants Sandstone Member found elsewhere and contain a shallow-marine fossil assemblage deposited in moderate depths (Saul, 1982:74). Detailed sedimentologic and paleoenvironmental studies are also lacking for this locality.

Saul (1986a:29) reported two fragments of a large thick-shelled ostreid from LACMIP loc. 26525 in the lower upper Maastrichtian El Piojo Formation in the vicinity of Lake Nacimiento [Area 13]. The largest fragment (height 68 mm) is a wedge morph. Its smooth exterior has been bored by bivalves, which is a common feature in specimens of *A. parasitica* found elsewhere. Kirby (1991:80, pl. 3, fig. 1) reported unidentifiable ostreid fragments from LACMIP loc. 14320 in a thin interval of uppermost Maastrichtian strata in the basal San Francisquito Formation in the Warm Springs Mountain area, Los Angeles County [Area 14]. Fossils in this part of the formation are generally not well preserved. He stated that one of the thin-shelled specimens might be a *Pycnodonte*, but it is *Amphidonte parasitica*.

Coquand (1869:63) believed that Gabb's *Exogyra parasitica* belonged in genus *Ostrea* and consequently a secondary homonym of *Ostrea parasitica* Gmelin, 1791. Coquand, incidentally, was not aware that the name *Ostrea parasitica* was first used by Lindroth, 1788. Gabb's species, however, does not belong in *Ostrea*; thus, Gabb's name is not a secondary homonym, and Stoliczka (1871:458) recognized this fact.

?*Amphidonte parasitica* (Gabb, 1864)

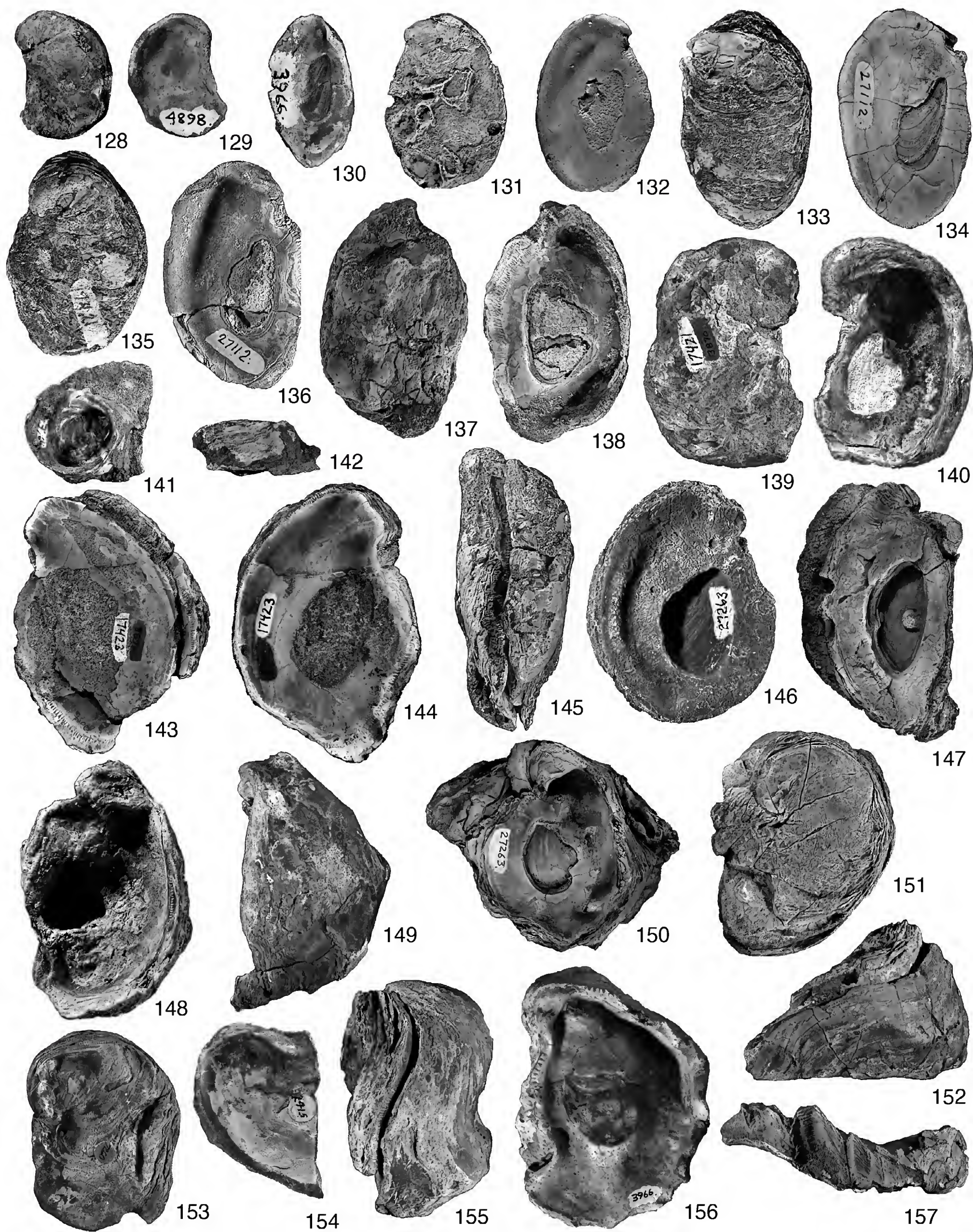
Figures 156, 157

REMARKS. A single and unusual left valve of ?*Amphidonte parasitica* (Figs. 156, 157) from LACMIP loc. 3966 in the Point Loma Formation, near Carlsbad, San Diego County, Southern California, is similar to the auriform morph of *A. parasitica* in terms of overall shape and adult size, anterior wall slightly higher than posterior wall, and large subcentral adductor muscle scar. This unusual specimen differs from *A. parasitica* by having prominent, angularly terminate wide plicae on the anterior wall, as well as obvious bourrelets, and catachomata present on only the dorsal half of both margins of the valve. In addition, the catachomata differ by being shorter, stronger, and similar shapes on both margins of the valve. This unusual specimen might represent another species. Although the presence of plicae on the ?*A. parasitica* specimen is indicative of placement in *Ceratostreon* Bayle, 1878, such a placement is unmerited because *Ceratostreon* has a much more spirally incurved ligamental area, as well as much weaker and longer catachomata.

Subfamily Pycnodontinae Stenzel, 1959

Genus *Pycnodonte* Fischer de Waldheim, 1835

Figures 114–127 *Costagyra* spp., PSNA region. **114–120.** *Costagyra californica* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16]. **114.** Holotype UCMP 12320, UCMP loc. 2143, left valve (very worn), height 57 mm, ×1. **115.** Hypotype LACMIP 14590, LACMIP loc. 8198, left valve, height 36.5 mm, ×0.9. **116–119.** Originally conjoined, LACMIP loc. 8198. **116.** Hypotype LACMIP 14591, left valve, height 52.6 mm, ×0.8. **117–119.** Hypotype LACMIP 14592, right valve, height 53.2 mm, ×0.8. **117.** Exterior. **118.** Interior. **119.** Posterior view. **120.** Hypotype LACMIP 14593, LACMIP loc. 24063, right valve, height 52.7 mm, ×1. **121–127.** *Costagyra garza* sp. nov., Moreno Formation, “Garzas Sand” [Area 11]. **121.** Paratype LACMIP 14595, LACMIP loc. 26358, left valve, height 51.9 mm, ×0.8. **122–124.** LACMIP loc. 10660, originally conjoined valves. **122.** Paratype LACMIP 14596, left valve, height 80.4 mm, ×0.8. **123.** Right valve interior, height 74.2 mm, ×0.8. **124.** Anterior view of reunited conjoined valves, thickness 76 mm. **125–127.** Holotype LACMIP 14594, LACMIP loc. 26517, conjoined valves, height 92.8 mm, ×0.7. **125.** Left valve. **126.** Right valve interior. **127.** Left valve, posterior side, thickness 49.7 mm.



TYPE SPECIES. *Pycnodonte radiata* Fischer de Waldheim, 1835, by original designation; Late Cretaceous, Crimea.

AGE AND DISTRIBUTION. Cretaceous to Holocene, with modest post-Cretaceous record and at least one extant species (Hayami and Kase, 1992); and widespread (Stenzel, 1971). The PSNA species revised here is the earliest report of *Pycnodonte* s.s. in the PSNA region.

REMARKS. In addition to *Pycnodonte* s.s., Stenzel (1971) recognized three subgenera of genus *Pycnodonte*: *Costeina* Vialov, 1965; *Crenostrea* Marwick, 1931; and *Phygraea* Vialov, 1936. Since Stenzel's work, two other subgenera were added: *Eupycnodonte* Freneix, 1979, and *Pegma* Squires and Demetrian, 1990. The subgeneric division of *Pycnodonte* has historically been controversial and confusing. Hayami and Kase (1992) commented that much of this confusion stems from not considering intraspecific variation and different modes of life.

Pycnodonte has been reported as an epifaunal-cemented bivalve (Ayoub-Hannaa and Fürsich, 2012:125), but species can have adults that lived as free-living, "cup-shaped" recliners in silty substrate (Wilmsen and Voigt, 2006). Morphology can be very variable, with shell form and size of attachment area strongly dependent on ecologic factors, as well as on ontogenic factors (e.g., duration of fixation) (Machalski, 1998). Its shell microstructure is vesicular ("honeycomb") (Jaitly et al., 2014).

Subgenus *Pycnodonte* s.s.

Pycnodonte (*Pycnodonte*) *malleiformis* (Gabb, 1864) comb. nov.

Figures 6, 14, 158–168

Ostrea malleiformis Gabb, 1864:204, pl. 31, fig. 272; White, 1884:297, pl. 50, fig. 7 (after Gabb); Jones et al., 1978:XXII.9, unfig.

"*Ostrea*" *malleiformis* Gabb. Stewart, 1930:131, pl. 3, fig. 10; text-fig. 3.

EMENDED DESCRIPTION. Shell size up to height 27 mm. Shell paper-thin, brittle, and fragile. Shape variable with three morphs: auriculate, spatulate, and suboval. Valves flattish, oblique poster-oventrally, slightly inequivalved, and nearly equilateral. Dorsal margin normally long and straight but can be short. Beaks small but distinct. Adductor muscle scar small, elliptical, and located posterior of center of valve. Shell microstructure vesicular but obscure. **Left valve:** Auricles on both sides of hinge; anterior auricle more distinct, projecting, and can be concave medially. Umbo rising barely above long, straight dorsal margin. Exterior commonly smooth, but growth lines can occur in distinct commarginal bands, widely or closely spaced. Attachment scar not obvious. Catomata sparse, located just anterior and posterior of

resilifer; only faint pits along anterior margin of shell. Interior smooth; rarely with rimmed, large circular hollow area underneath umbo. **Right valve:** Fits within slightly larger left valve and is concave (sunken). Exterior smooth with extremely fine (microscopic) and closely spaced growth lines. Interior smooth. Anachomata very small, moderately spaced along most of posterior side up to hinge, and some on anterior side near hinge.

NEOTYPE. ANSP 4433 (designated by Stewart, 1930:131), height 38 mm, length 27 mm, Cottonwood Creek, Siskiyou County, Northern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. Jacksonville, Jackson County, southwest Oregon [Area 3] to east of Redding, Northern California [Area 5].

STRATIGRAPHIC DISTRIBUTION. ?Hornbrook Formation: Jacksonville, Jackson County, southwest Oregon (Gabb, 1864); Yreka area, Siskiyou County, Northern California (Stewart, 1930); Redding Formation, Bella Vista Sandstone Member and Frazier Siltstone Member, Dry Creek, east of Redding, Shasta County, Northern California (Jones et al., 1978).

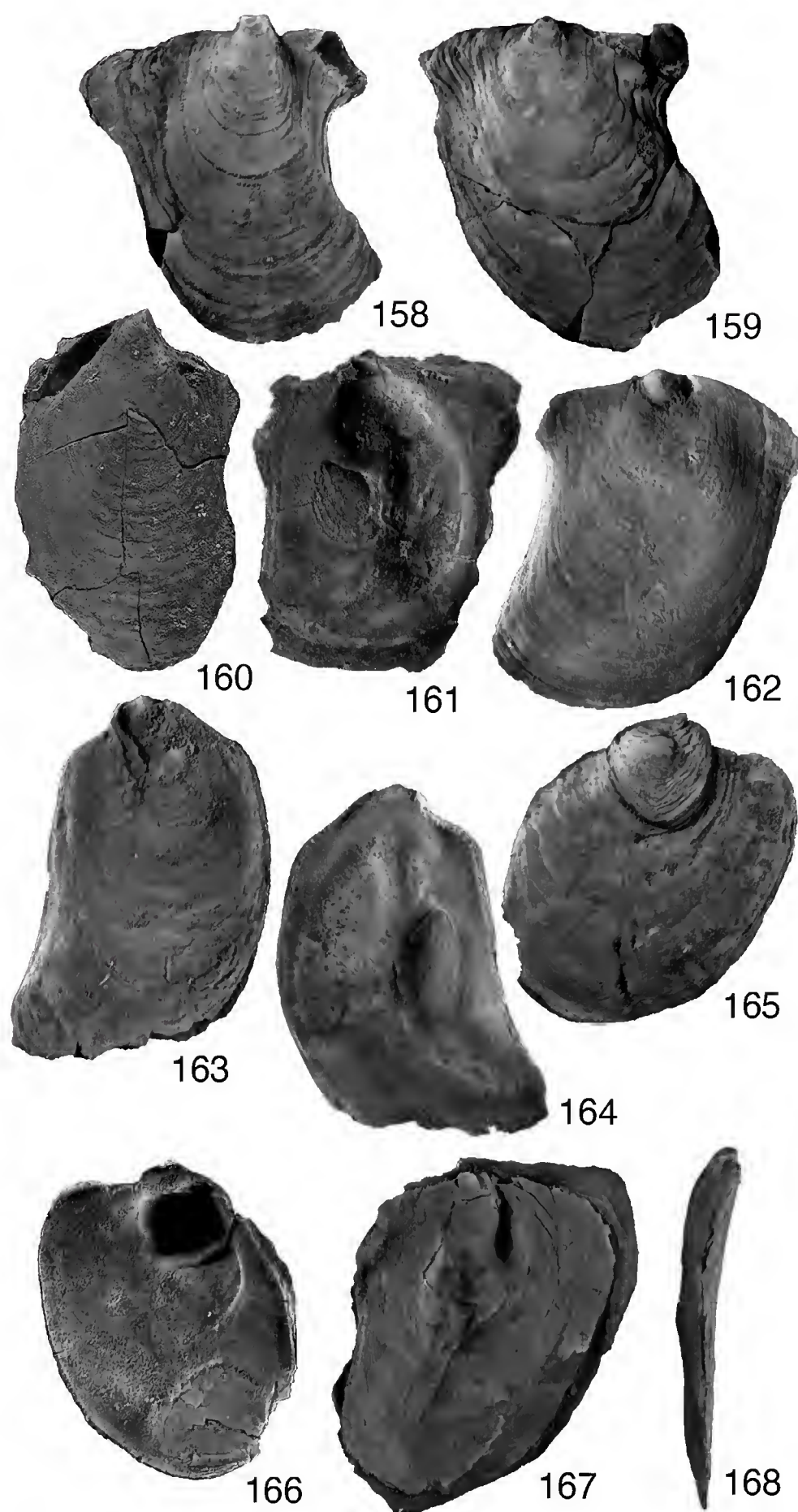
REMARKS. One hundred and twenty-eight specimens were examined. Both left and right valves are equally represented, and some are conjoined. Preservation of many specimens is excellent. The valves of *malleiformis* are most similar to those of the type species *Pycnodonte* (*P.*) *radiata*, as described by Stenzel (1971:N1107). The similarities are the left valve umbo rising barely above the long, straight dorsal margin; auricles present; radial ribs absent; and concentric puckers and welts absent. The valves of *malleiformis* differ by not being circular nor subcircular, and its chomata are not vermiculate.

Pycnodonte (*P.*) *malleiformis* is very similar in morphology to the extant *Pycnodonte* (*P.*) *taniguchii* Hayami and Kase (1992:1076–1082, figs. 2–7) from shallow depths (20–30 m) in several poorly lighted submarine caves (i.e., cryptic, sheltered habitat) of Miyako and Okinawa Islands, southern Japan. This oyster seems to adhere to cave walls via attachment of the left valve. According to Hayami and Kase (1992:1081), *P.* (*P.*) *taniguchii* is closely similar to *P.* (*P.*) *radiata*. *Pycnodonte* (*P.*) *malleiformis* differs from *P.* (*P.*) *taniguchii* by having a much smaller size, much flatter left valve, and absence of a well-defined commissural shelf.

Genus *Phygraea* Vialov, 1936

TYPE SPECIES. *Gryphaea pseudovesicularis* Gümbel, 1861, by original designation; late Paleocene, Austria.

Figures 128–157 *Amphidonte* and ?*Amphidonte*, Point Loma Formation [Area 17], unless otherwise noted. **128–154.** *Amphidonte parasitica* (Gabb, 1864). **128–129.** Hypotype LACMIP 14598, LACMIP loc. 4898, right valve, height 17 mm, $\times 1.4$. **128.** Exterior. **129.** Interior. **130.** Hypotype LACMIP 14599, LACMIP loc. 3966, right valve interior, height 20 mm, $\times 1.4$. **131–132.** Plastolectotype ANSP 4429, Chico Formation [Area 9], right valve, height 39.2 mm, $\times 0.8$. **131.** Exterior. **132.** Interior. **133–134.** Hypotype LACMIP 14600, LACMIP loc. 27112, right valve, height 43 mm, $\times 0.9$. **133.** Exterior. **134.** Interior. **135.** Hypotype LACMIP 14601, LACMIP loc. 17421, right valve, height 37.2 mm, $\times 1$. **136.** Hypotype LACMIP 14602, LACMIP loc. 27112, right valve interior, height 43 mm, $\times 1$. **137–138.** Hypotype LACMIP 14603, LACMIP loc. 3966, left valve, height 57.3 mm, $\times 0.8$. **137.** Exterior. **138.** Interior. **139–140.** Hypotype LACMIP 14604, LACMIP loc. 17421, height 58.1 mm, $\times 0.7$. **139.** Exterior. **140.** Interior. **141–142.** Hypotype LACMIP 14605, LACMIP loc. 3966, diameter 25.2, height 10.8, $\times 0.8$. **141.** Top view. **142.** Side view. **143–145.** LACMIP loc. 17423, originally conjoined valves. **143.** Hypotype LACMIP 14606, left valve interior, height 65 mm, $\times 0.7$. **144.** Hypotype LACMIP 14607, right valve interior, height 70 mm, $\times 0.7$. **145.** Anterior view of previous two hypotypes shown conjoined, thickness 24 mm. **146.** Hypotype LACMIP 14608, LACMIP loc. 27263, Rosario Formation [Area 19], right valve interior, height 60.2 mm, $\times 0.7$. **147.** Hypotype LACMIP 14609, LACMIP loc. 27263, Rosario Formation [Area 19], right valve interior, height 80.6 mm, $\times 0.6$. **148–149.** Hypotype LACMIP 14610, LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 17], left valve, height 73.4 mm, $\times 0.6$. **148.** Interior. **149.** Anterior view, thickness 43 mm. **150.** Hypotype LACMIP 14611, LACMIP loc. 27263, Rosario Formation [Area 20], left valve interior cemented to right valve exterior of *Acutostrea taxidonta*, height 63 mm, $\times 0.6$. **151–152.** Hypotype LACMIP 14612, LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 16], conjoined valves, height 58.3 mm, $\times 0.7$. **151.** Right valve. **152.** Anterior side of conjoined valves, thickness 32 mm. **153.** Hypotype LACMIP 14613, LACMIP loc. 27260, Rosario Formation [Area 19], right valve, height 57.2 mm, $\times 0.6$. **154–155.** LACMIP loc. 22415, Williams Formation, Pleasants Sandstone Member, Bee Canyon [Area 16], originally conjoined valves. **154.** Hypotype LACMIP 14614, partial right valve interior, height 44.2 mm, $\times 0.8$. **155.** Hypotype LACMIP 14615, anterior side of reunited conjoined valves, height 53.4 mm, thickness 34 mm, $\times 0.8$. **156–157.** ?*Amphidonte parasitica* (Gabb, 1864), hypotype LACMIP 14616, LACMIP loc. 3966, left valve, height 58.8 mm, $\times 0.8$. **156.** Interior. **157.** Anterior side.



Figures 158–168 *Pycnodonte (Pycnodonte) malleiformis* (Gabb, 1864), Redding Formation, Frazier Siltstone Member [Area 5], unless otherwise noted. **158.** Hypotype LACMIP 14617, LACMIP loc. 24214, left valve, height 25.9 mm, $\times 1.4$. **159.** Hypotype LACMIP 14618, LACMIP loc. 10730, Redding Formation, Bellavista Sandstone Member [Area 5], left valve, height 25.5 mm, $\times 1.4$. **160.** Hypotype LACMIP 14619, LACMIP loc. 24214, left valve, height 29.2 mm, $\times 1.3$. **161.** Hypotype LACMIP 14620, LACMIP loc. 24214, left valve interior, height 25.5 mm, $\times 1.4$. **162.** Hypotype LACMIP 14621, LACMIP loc. 24214, right valve, height 22.1 mm, $\times 1.6$. **163–164.** Hypotype LACMIP 14622, LACMIP loc. 24214, right valve, height 22.2, $\times 1.7$. **163.** Exterior. **164.** Interior. **165–166.** Hypotype LACMIP 14623, LACMIP loc. 24214, right valve, height 27 mm, $\times 1.2$. **165.** Exterior. **166.** Interior. **167–168.** Hypotype LACMIP 14624, LACMIP loc. 24214, conjoined valves, height 24.5 mm, $\times 1.5$. **167.** Right valve. **168.** Posterior view, thickness 3.6 mm.

AGE AND DISTRIBUTION. Cretaceous to Miocene and widespread (Stenzel, 1971). The species revised here and the new species named below are the first reports of Cretaceous *Phygraea* in the PSNA region. *Phygraea* is represented by several species in Paleocene and lower Eocene strata in California (Squires and Demettrion, 1994).

REMARKS. As mentioned above, the subgeneric division of *Pycnodonte* has been controversial. It is especially confusing in regard to how *Pycnodonte* s.s. differs from *Phygraea*. Many modern workers (e.g., Malchus, 1990; Hayami and Kase, 1992; Malchus et al., 1994; Seeling and Bengtson, 1999; Wilmsen and Voigt, 2006) have followed the traditional view of Stenzel (1971) in placing *Phygraea* as a subgenus of *Pycnodonte*. Cooper (1992), Jaitly and Mishra (2001), and Jaitly et al. (2014), however, treated *Phygraea* as a distinct genus, and their practice is followed here.

The posteroventral flange of *Phygraea* most likely provided stability on soft sediments. Even at single localities there can be much morphologic variation, which represents polymorphic populations rather than allopatric or chronologic species/subspecies (Wilmsen and Voigt, 2006:23).

Phygraea inornata (Packard, 1922) comb. nov.

Figures 7, 169–187

Exogyra inornata Packard, 1922:420, pl. 27, fig. 1.

EMENDED DESCRIPTION. Shell size up to 66 mm height. Shell thin and smooth. Shape variable with three morphs: narrow, wide, and truncated spatulate. All strongly inequivalved. No auricles. Both valves smoothish. Adductor muscle scar small and off-center. Shell microstructure vesicular, in thin layers. **Left valve:** Juvenile and early adult specimens of narrow morph with umbo compressed, prominent, and tapered; beak straight, incurved (either anteriorly or posteriorly), and rising well above hinge. Adult narrow-morph specimens rarely have wide umbo, distinct posteroventral flange, and pseudo-auricle on anterodorsal region where attachment area intersects side of valve. Truncated-spatulate morph similar to narrow morph but with truncated umbo; umbo and beak replaced by small to large concavity (bowl-like) or flattened to bulging region representing attachment area on anterodorsal part of shell; ridgelets, welts, or puckers can be present adjacent to attachment area. Attachment scar not obvious. Catagomata on truncate-spatulate morph simple, short, and only on dorsal half of both shell margins. **Right valve:** Lowly concave to lid-like. Commarginal shelf can be present. Anachomata on both narrow and truncated-spatulate morphs short, vermiculate, and only on dorsal half of both shell margins.

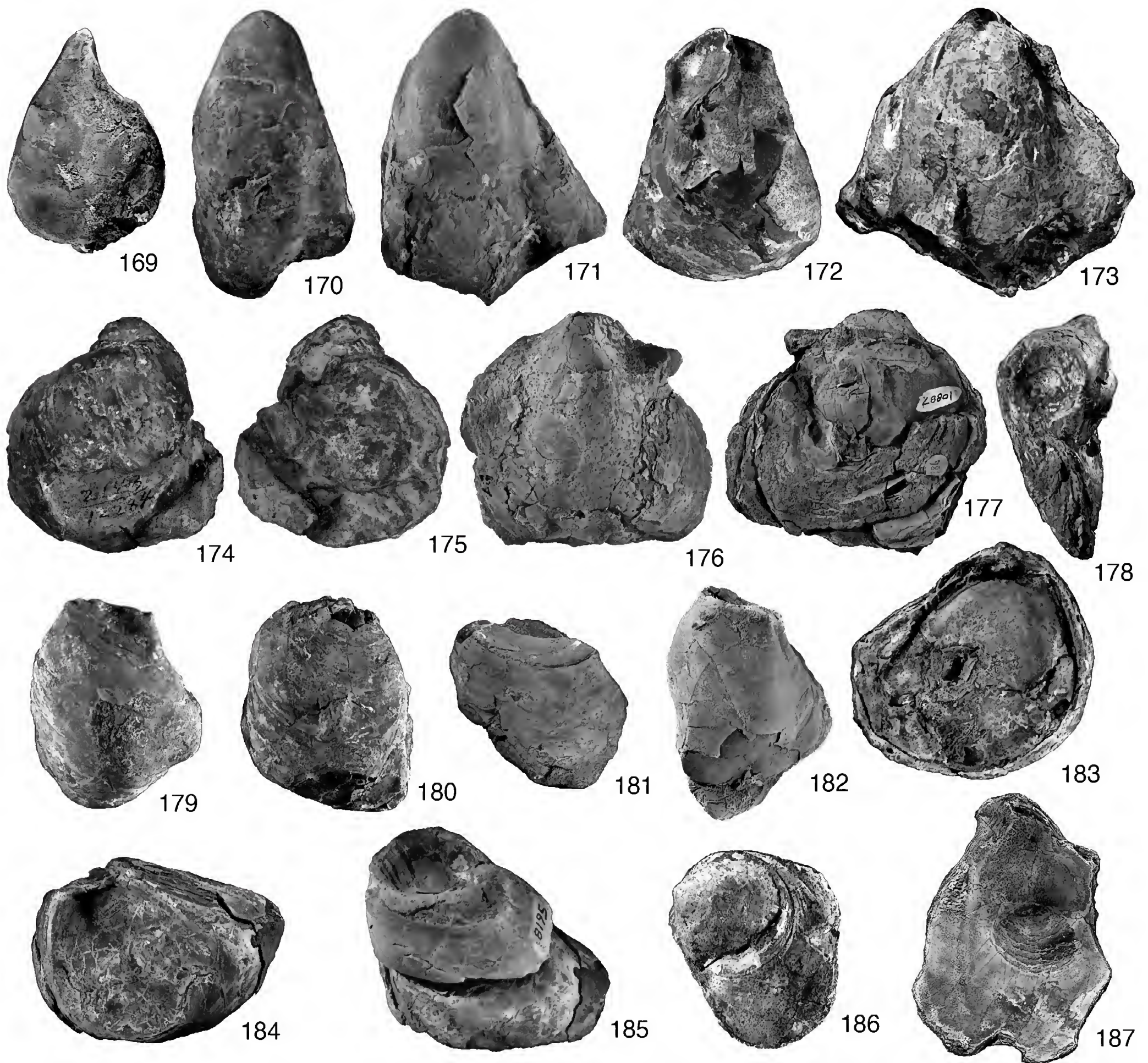
HOLOTYPE. Holotype UCMP 12284, height 35 mm, length 33.8 mm, UCMP loc. 2143, Ladd Formation, Baker Canyon Member, Silverado Canyon, Santa Ana Mountains, Orange County, Southern California.

GEOLOGIC AGE. Turonian.

GEOGRAPHIC RANGE. East of Redding, Shasta County, Northern California [Area 5] to Santa Ana Mountains, Orange County, Southern California [Area 16].

STRATIGRAPHIC DISTRIBUTION. Redding Formation, Frazier Siltstone Member, tributary to Dry Creek, Shasta County, Northern California (new occurrence); Ladd Formation, Baker Canyon Member, Black Star Canyon and east side of Silverado Canyon, Santa Ana Mountains, Orange County, Southern California (Packard, 1922).

REMARKS. Three hundred and fifty specimens were examined. Nearly all of them are left valves, and their preservation is moderately good. Right valves and conjoined valves are scarce and poorly preserved. Specimens are encased in hard siltstone or in poorly sorted silty fine-



Figures 169–187 *Phygraea inornata* (Packard, 1922), Ladd Formation, Baker Canyon Member [Area 16], unless otherwise noted. **169.** Hypotype LACMIP 14625, LACMIP loc. 24654, Redding Formation, Frazier Siltstone Member [Area 5], left valve, height 21.1 mm, $\times 1.7$. **170.** Hypotype LACMIP 14626, LACMIP loc. 8195, left valve, height 38.4 mm, $\times 1.2$. **171.** Hypotype LACMIP 14627, LACMIP loc. 8195, left valve, height 42.4 mm, $\times 0.9$. **172.** Hypotype LACMIP 14628, LACMIP loc. 8195, left valve, height 37 mm, $\times 1$. **173.** Hypotype LACMIP 14629, LACMIP loc. 16857, left valve, height 55.6 mm, $\times 0.8$. **174–175.** Holotype UCMP 12284, UCMP loc. 2143, left valve, height 35 mm, $\times 1$. **174.** Exterior. **175.** Interior (mostly infilled with matrix). **176–178.** Hypotype LACMIP 14630, LACMIP loc. 10887, conjoined valves, height 59.5 mm, $\times 0.6$. **176.** Left valve. **177.** Right valve. **178.** Posterior side, thickness 32.7 mm. **179.** Hypotype LACMIP 14631, LACMIP loc. 8195, left valve, height 26.3 mm, $\times 1.3$. **180.** Hypotype LACMIP 14632, LACMIP loc. 8195, left valve, height 33.8 mm, $\times 1$. **181.** Hypotype LACMIP 14633, LACMIP loc. 8195, left valve, height 38.9 mm, $\times 0.7$. **182.** Hypotype LACMIP 14634, LACMIP loc. 8195, left valve, height 42.4 mm, $\times 0.9$. **183–185.** LACMIP loc. 10959, originally conjoined valves. **183.** Hypotype LACMIP 14635, left valve interior, height 28.5 mm, $\times 1.3$. **184.** Hypotype LACMIP 14636, right valve interior, height 28.4 mm, $\times 1$. **185.** Oblique anterior view of previous two hypotypes shown conjoined, left valve above, right valve below, combined thickness of valves 25 mm, $\times 1.4$. **186.** Hypotype LACMIP 14637, LACMIP loc. 24654, Redding Formation, Frazier Siltstone Member [Area 5], right valve, height 30.7 mm, $\times 1$. **187.** Hypotype LACMIP 14638, LACMIP loc. 8195, right valve interior, height 25 mm, $\times 1.7$.

grained sandstone, and the majority of them are from the Baker Canyon Member. Shell exteriors are decorticated on many specimens. Chomata are rarely preserved, and most are preserved on internal casts. The vesicular microstructure has been filled in with secondary calcite.

Two views of the holotype are figured here (Figs. 174, 175). Packard (1922) mentioned a “cotype” of his species but did not assign a catalog number. The whereabouts of this “cotype” are unknown. Representative interiors of the valves of *P. inornata* are shown here for the first time (Figs. 183, 184, 187).

The morphs of *P. inornata* are not restricted geographically nor stratigraphically, and this information is strongly suggestive that they are the result of ecophenotypic factors rather than evolution (i.e., separate species). For example, these polymorphic populations occur in the Redding Formation, Shasta County, Northern California (LACMIP loc. 24654), and in the Baker Canyon Member, Orange County, Southern California (LACMIP loc. 8195). The relative abundance of each morph, however, can differ from locality to locality. Most of the narrow-morph specimens of *P. inornata* show no attachment scar, but a rare specimen from locality 8195 (Fig. 172) has a small shell attached to its umbo. Also, most of the wide-morph specimens do not show an attachment scar. A particularly wide specimen (Figs. 176–178) from LACMIP loc. 10887 in the Baker Canyon Member has a moderately large attachment scar creating a pseudo-auricle. The truncated-spatulate morph specimens all show attachment scars on the left valve. The shape of *P. inornata*, therefore, was largely controlled by whether there was attachment to a foreign object.

As mentioned earlier, *P. inornata* co-occurs with *C. crescentica* and *C. californica* at various localities in the Baker Canyon Member of the Ladd Formation, Santa Ana Mountains, Orange County, Southern California.

***Phygraea arida* sp. nov.**

Figures 11, 188–199

DIAGNOSIS. Shell size large. Shape variable but predominantly circular. Shell smooth, flattish, moderately thick, and heavy. Left valve with slight genticulation posterior to umbo region and with tongue-like flange extending from posterocentral region. Right valve low convex anteriorly, concave posteriorly, with well-developed commissural shelf.

DESCRIPTION. Shell size up to height 95 mm. Shell moderately thick and heavy. Shape variable with three morphs: circular, truncated spatulate, and subtrigonal. Circular morph common, other morphs rare. Umbo and beak mostly improminent, except projected beak on subtrigonal morph. Dorsal margin long, rarely short. Valves smooth (no radial ribs). Adductor muscle scar moderate size, circular, nearly central but somewhat near hinge. Catachomata and anachomata only near hinge and vermiculate (lath-like). Commissural shelf prominent, delimited proximally by circumferential curb. Shell microstructure vesicular (“foamy”) with several thin to thick layers (individually up to 8 mm thick) separated from each other by thin horizontal lamellae. **Left valve:** Juvenile shell area of circular morph inflated; adult circular morph with prominent tongue-like flange extending from posterocentral region, and anteroventral part of interior of valve concave; commissural shelf on larger specimens close to muscle scar and to prominently raised posterior of muscle scar. **Right valve:** Lowly convex (inflated) along anterior side and concave posteroventrally; umbo area can be swollen. Adductor muscle scar near posterior, anachomata along dorsal anterior and dorsal posterior regions. Commissural shelf occurs as raised narrow curb along anterior margin and occurs as much broader swollen area along most of posterior side, including posterior side of adductor muscle scar.

HOLOTYPE. Holotype LACMIP 14639, height 81.3 mm, length 89.2 mm, LACMIP loc. 10685, Los Banos Creek, Moreno Formation, “Quinto Silt,” Los Banos Creek, Merced County, Northern California.

PARATYPES. LACMIP 14640–14642; RBCM.EH2016.001.0001.001, RBCM EH.2016.001.0002.001, and RBCM.EH2016.002.0001.001.

GEOLOGIC RANGE. Late middle Campanian to late early to early late Maastrichtian.

GEOGRAPHIC RANGE. Denman Island, Vancouver Island, British Columbia, Canada [Area 1], to Garzas Creek, Merced County, Northern California [Area 11].

STRATIGRAPHIC DISTRIBUTION. UPPER MIDDLE CAMPANIAN: Upper Cedar District Formation, “White House” site, western Denman Island, off east coast of Vancouver Island, British Columbia, Canada [*Metaplaenticeras* cf. *pacificum* ammonite zone (see Ward et al., 2015:fig. 7)]. UPPER LOWER TO LOWER UPPER MAASTRICHTIAN: Moreno Formation, Tierra Loma Shale, “Garzas Sand,” and “Quinto Silt,” Garzas Creek, Merced County, west side of San Joaquin Valley, Northern California.

REMARKS. Thirty specimens were examined, including one conjoined-valved specimen. Preservation is generally excellent. Some of the Moreno Formation specimens are fragments. All the specimens (10) from the upper Cedar District Formation are small size, whereas those from California are much larger. *Phygraea arida* co-occurs with *A. parasitica* in the Cedar District Formation at the “White House” site on western Denman Island, British Columbia, Canada.

Most specimens of *P. arida* were probably soft-sediment recliners, based on absence of any attachment scar. A small-sized, single left valve from the upper Cedar District Formation, however, is strongly cemented to an echinoid spine (Fig. 199).

The new species differs from *P. inornata* by having a much larger and heavier shell, well developed commissural shelf on many specimens, discernible “foamy” texture, orbicular shape on most specimens, stronger vermiculate chomata, no overhanging or twisted beaks, and no radial sulcus.

The new species is very similar to the *Pycnodonte* (*Pycnodonte*) *gigantica* (Solander, 1766:36, fig. 88). Solander’s species was originally named *Ostrea gigantica* and was the type species of *Gigantostrea* Sacco (1897:14, pl. 4) from Eocene strata in Italy. The new species differs from *P. (P.) gigantica* by having a tongue-like flange extending centroposteriorly from the left valve. Stenzel (1971) equated *Gigantostrea* with *Pycnodonte* (*Pycnodonte*), but his usage is not followed here.

ETYMOLOGY. The new species name is derived from *aridus* (Latin, dry), in reference to Laguna Seca (Spanish, dry lake) Creek.

PALEOGEOGRAPHY AND PALEOCLIMATE COMMENTS

The PSNA region makes up a large part of Kauffman’s (1973:fig. 1) Cretaceous bivalve-based “Northeast Pacific Subprovince” of the “North Pacific Province,” which was part of the “North Temperate Realm.” A temperate realm for this area has been corroborated by faunal studies of a wide array of mollusk groups (Saul, 1986b; Kiel, 2002), including neritid and cypraeoidean gastropods (Squires et al., 2001), nerineid gastropods (Saul and Squires, 1998; Saul and Squires, 2002), volute gastropods (Saul and Squires, 2008), and opine bivalves (Squires and Saul, 2009). These studies provide ample evidence that the “Northeast Pacific Subprovince,” in the area of this present report, experienced warm-temperate waters during much of the Late Cretaceous. In addition, *Coralliochama orcutti*, a warm-water rudist bivalve (Saul, 1986b), co-occurs with *A. parasitica* in four formations in PSNA: 1) Gualala Formation, Anchor Bay Member, Mendocino County (Elder et al., 1998); 2) Williams Formation, Pleasants Sandstone Member (LACMIP loc. 22415, Bee Canyon, Santa Ana Mountains, Orange County); 3) basal Point Loma Formation (vicinity of LACMIP loc. 17421, Carlsbad, San Diego County); and 4) Rosario Formation (LACMIP loc. 27263,

San Antonio del Mar, Baja California, Mexico). The warm-temperate *A. parasitica* is one of most common PSNA oysters of Campanian to Maastrichtian age and has the widest geographic range, from British Columbia to Northern Baja California. In Europe, *Amphidonte* is also a warm-temperate oyster and not reported from Tethyan (tropical) locales in that region (Aqrabawi, 1993).

None of the PSNA Late Cretaceous oyster genera are endemic to the "Northeast Pacific Subprovince." They are all widespread genera, and, using Kauffman's (1973:359) bivalve categories, *Rastellum* [= *Arctostrea*], *Crassostrea*, and *Pycnodonte* are "truly cosmopolitan forms." Although Stenzel (1971:N1107) reported the geographic distribution of *Pycnodonte* (*Pycnodonte*) to be worldwide, Hayami and Kase (1992:1076) noted that Cretaceous, as well as Paleogene, species of this oyster are known almost exclusively from low-middle latitudinal regions; namely, western Europe, Crimea, north and west Africa, south India, and Gulf Coast regions. The PSNA region can now be added to this list. *Phygraea* was widely distributed in both temperate and tropical (Tethyan) waters, and this oyster has diminished value for paleogeographic purposes (Aqrabawi, 1993).

BIODIVERSITY COMMENTS

During Late Cretaceous time, the world experienced greenhouse climate conditions, and the late Cenomanian and early Turonian interval coincided with the Cretaceous thermal maximum and highest sea levels. The Turonian-Coniacian turnover event, which coincided with a global drop in sea level, was a cool time that persisted during Coniacian time. Although there was a modest warming in early Santonian time, cool-water conditions returned during the late Santonian. During Campanian time, there were fluctuations in sea surface temperatures and sea level, but there was an overall warming trend and a sea level rise that culminated during early Maastrichtian time (Forster et al., 2007:fig. 2; Miller et al., 2011:fig. 4; Linnert et al., 2014:fig. 2).

The PSNA Late Cretaceous oyster fauna (Fig. 2) had a high biodiversity level (five species) during Turonian time. This was followed by a dramatic drop (zero species) during the Coniacian, a low level (one species) near the end of the Santonian, and a mostly gradual buildup during the Campanian. The highest biodiversity level (six species) occurred in the late early to early late Maastrichtian, followed by a continuing high level (five species) during the late Maastrichtian. This overall biodiversity pattern is very similar to that of Late Cretaceous neritid and cypraeoidean gastropods in the PSNA region (Squires et al., 2001).

A rigorous analysis of the causes of the observed biodiversity pattern in the PSNA Late Cretaceous oysters is beyond the scope of this paper. Some possible explanations include 1) global changes in ocean surface water temperatures, 2) global changes in sea level, 3) closure of seaways, 4) tectonic influences associated with the active plate margin that existed in the PSNA region, and 5) collecting/sampling artifacts. The available evidence is indicative, however, that warm surface waters during the Turonian, Campanian, and Maastrichtian would have favored the thermophilic oysters, and the accompanying high sea levels would have provided more habitats and the best potential for burial of the nearshore oysters. The abrupt drop of diversity at the end of the Turonian was most likely related to the influx of cooler waters. The cooler surface waters, reduced potential for habitats, and pervasive on-going erosion of nearshore deposits associated with the lower sea levels during the Coniacian and Santonian could have been responsible for the paucity of oyster taxa. The PSNA oyster species that originated during the Campanian went extinct at various times, thereby indicating more gradual and short-lived changes in temperature.

In the PSNA region, there was a reoccurrence of the warm-water Turonian *Curvostrea*-*Costagyra*-*Phygraea* association in the late early to early late Maastrichtian. This reoccurrence is very strongly indicative that warm temperature and high sea level were largely responsible for the highest diversities of PSNA oysters.

In his work on Late Cretaceous oysters in Jordan, Aqrabawi (1993) reported a biodiversity pattern similar to that of the PSNA region, in that there are no oyster taxa of Coniacian age and there is low biodiversity in the Santonian, in contrast to much higher biodiversity before and after these times. He also reported a similar pattern for Late Cretaceous oysters from northwest Europe. For both areas, he provided no evidence as to what caused the observed patterns, although he did mention, for northwest Europe, that transgressions and regressions were responsible.

CONCLUSIONS

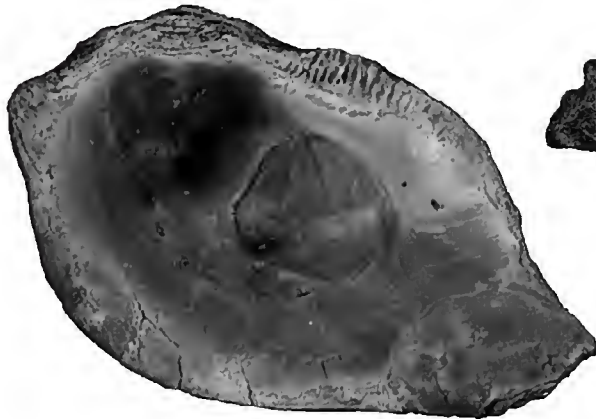
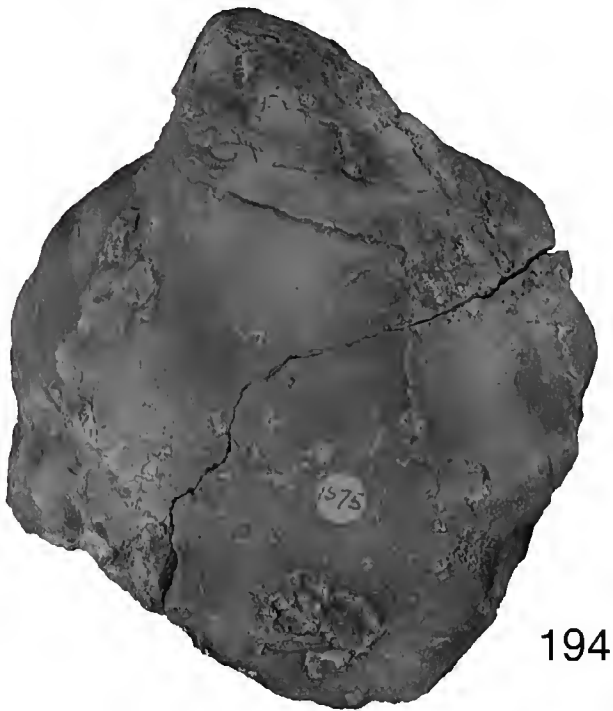
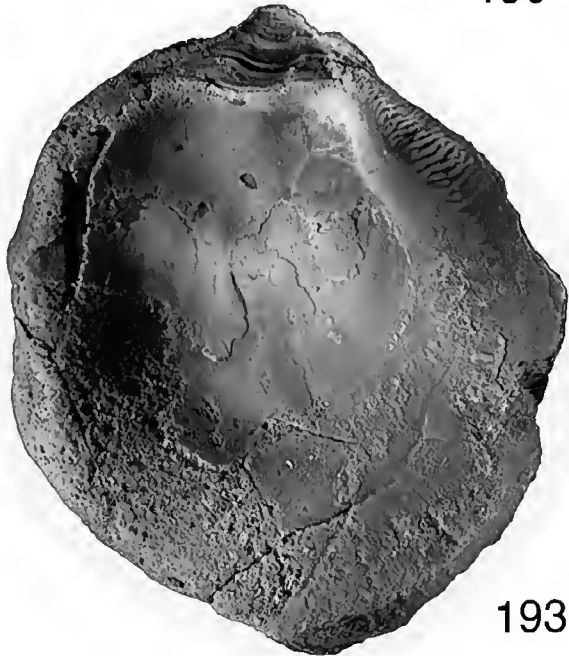
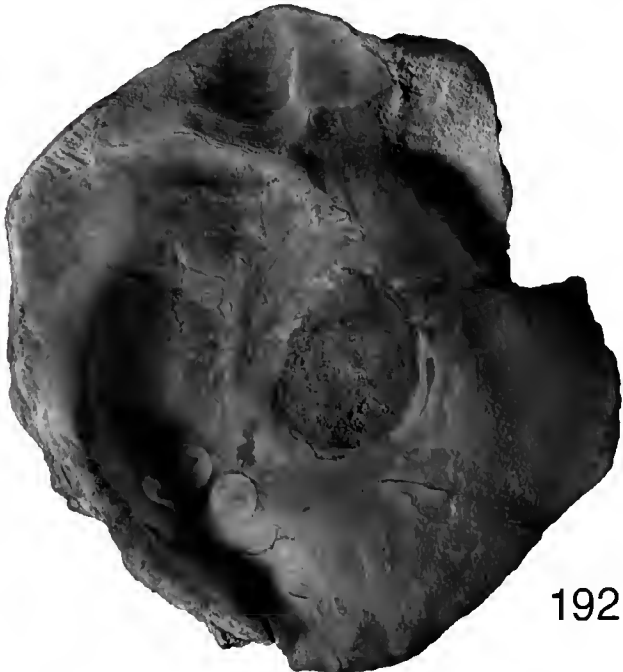
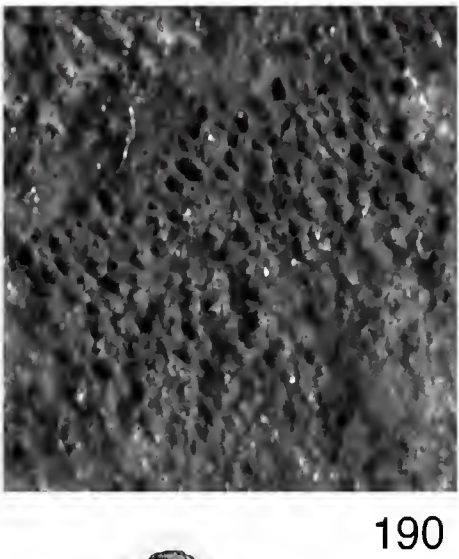
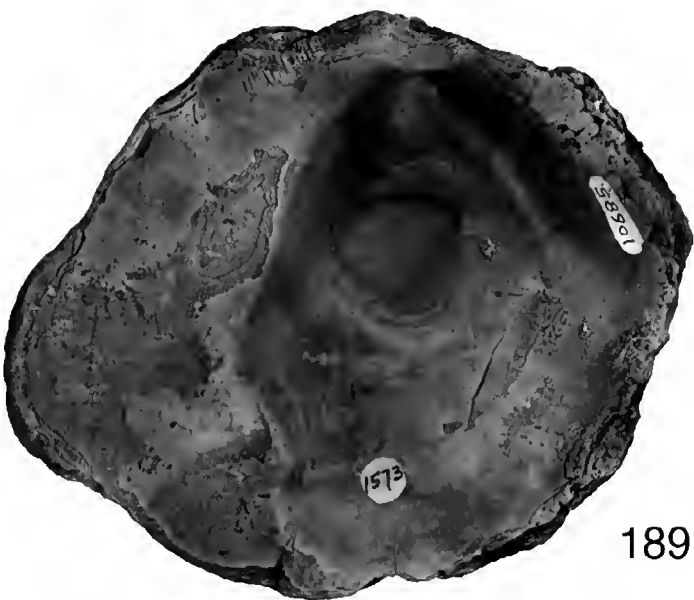
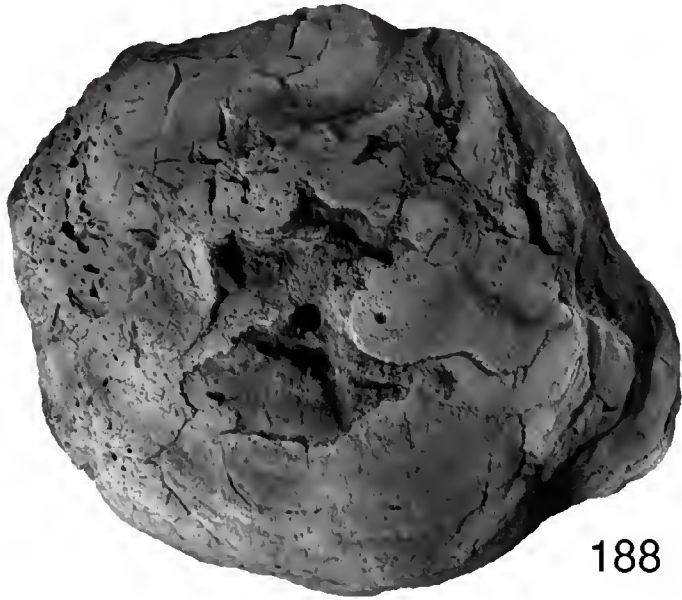
During the course of revising the seven previously named oyster species from the warm-temperate Late Cretaceous "Northeast Pacific Subprovince," four new, one unnamed, and one questionable species were recognized, thereby resulting in a total of 13 species. All seven of the previously named species belong to genera different from those Gabb (1864) and Packard (1922) assigned. The revised identifications are: *Curvostrea crescentica* (Packard, 1922); *Acutostrea taxidonta* (Packard, 1922); *Crassostrea brewerii* (Gabb, 1864); *Costagyra californica* (Packard, 1922); *Amphidonte parasitica* (Gabb, 1864); *Pycnodonte* (*P.*) *malleiformis* (Gabb, 1864); and *Phygraea inornata* (Packard, 1922). The *Amphidonte parasitica* (Gabb) identification was recognized previously by Elder (1991) and is confirmed here. An unusual specimen of ?*Amphidonte parasitica* is mentioned and figured here because it might represent another species.

The four new species are *Oscillopsa popenoei*, *Curvostrea baia*, *Costagyra garza*, and *Phygraea arida*. The one unnamed species is *Rastellum* sp., aff. *R. macropterum* (J.D.C. Sowerby, 1825). *Oscillopsa popenoei* is the first known occurrence of this genus in North America, and *Rastellum* is the first known occurrence of this genus in the PSNA region.

Genera represented by a single species are *Oscillopsa*, *Rastellum*, *Acutostrea*, *Crassostrea*, and *Pycnodonte* (*Pycnodonte*). Those represented by two species are *Curvostrea*, *Costagyra*, possibly *Amphidonte*, and *Phygraea*. All the oyster genera were globally widespread, and none were endemic to the PSNA region.

Amphidonte has the longest geologic range in the PSNA region, from early Campanian to questionably latest Maastrichtian. The species of *Oscillopsa*, *Rastellum*, *Curvostrea*, *Acutostrea*, *Crassostrea*, *Costagyra*, and *Phygraea* were relatively short lived. *Phygraea inornata* is the most abundant Late Cretaceous PSNA oyster. *Crassostrea brewerii* is the largest species, with its thick and heavy large specimens, which were commonly bored by large specimens of the bivalve *Lithophaga*. The PSNA Turonian species of *Curvostrea*, *Costagyra*, and *Phygraea* are much smaller than their early Maastrichtian species.

Nearly every Late Cretaceous PSNA oyster species has several morphs, which are most likely ecophenotypic responses related to changes in the paleoenvironments or related to the presence or absence of an attachment scar. In the case of *A. taxidonta*, the outline of its shell is dependent on the size of the attachment scar. Trigonal specimens have a small attachment scar, spatulate specimens have a large attachment scar, and oval specimens have an even larger attachment scar. It is likely that the larger the size of the attachment scar, the more agitated the waters were that the specimens lived in. In the case of *P. inornata*, whether or not there was attachment to a foreign object directly affected the shape of the individuals. Other species (e.g., *Crassostrea brewerii*) might also be represented by ecophenotypes, but the number of



specimens is too low to confirm this. Xenomorphism was most commonly observed in valves of *Acutostrea taxidonta*. A growth series was detected for *A. parasitica*.

The highest biodiversity levels of PSNA oysters (five to six species), which occurred during warm-temperate times and high sea levels (Turonian and late early to early late Maastrichtian), stand in stark contrast to a much lower biodiversity level (either no species or only one) during cooler times (Coniacian and Santonian, respectively). In the PSNA region, there was a reoccurrence of the Turonian warm-water *Curvostrea-Costagyra-Phygraea* association during the warm-water times of the late early to early late Maastrichtian. The PSNA oyster biodiversity pattern needs further study, but the available evidence is strongly indicative that global fluctuations in surface water temperature and contemporaneous sea level changes were most likely the controlling forces.

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LITERATURE CITED

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Figures 188–199 *Phygraea arida* sp. nov., Moreno Formation [Area 11], unless otherwise noted. **188–190**. Holotype LACMIP 14639, LACMIP 10685, left valve, height 81.3 mm. **188**. Exterior, ×0.6. **189**. Interior, ×0.6. **190**. Close-up of vesicular shell microstructure, posteroventral edge of valve, height 18.5 mm, ×10. **191–192**. Paratype LACMIP 14640, LACMIP loc. 26349, right valve, height 83.8 mm, ×0.7. **191**. Exterior. **192**. Interior. **193**. Paratype RBCM.EH.2016.001.0001.001, upper Cedar District Formation [Area 1], right valve interior, height 30.6 mm, ×1.9. **194**. Paratype LACMIP 14641, LACMIP loc. 10677, right valve, height 90.3 mm, ×0.7. **195–196**. Paratype LACMIP 14642, LACMIP loc. 22588, partial right valve, height 80.4 mm, ×0.7. **195**. Exterior. **196**. Interior. **197–198**. Paratype RBCM.EH.2016.001.0002.001, upper Cedar District Formation [Area 1], right valve, height 12.3 mm, ×2.9. **197**. Exterior. **198**. Interior. **199**. Paratype RBCM.EH.2016.002.0001.001, upper Cedar District Formation [Area 1], right valve attached to echinoid spine, valve height 27 mm, ×1.1.

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LATE MIOCENE BATS FROM THE JURUÁ RIVER, STATE OF ACRE, BRAZIL, WITH A DESCRIPTION OF A NEW GENUS OF THYROPTERIDAE (CHIROPTERA, MAMMALIA)¹

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ABSTRACT. We describe a new genus and species of thyropterid bat, *Amazonycteris divisus*, based on an isolated M¹ from upper Miocene deposits cropping out along the Juruá River in western Amazonia. The new taxon lacks a parastyle and stylocone on M¹, a unique derived condition among bats, but otherwise reflects the same M¹ morphology as other thyropterids. The unusual morphology of the specimen suggests a greater than expected diversity within the Family Thyropteridae. A second bat specimen from the same locality is referred to Molossidae genus and species indeterminate.

INTRODUCTION

Collectively, Neogene sedimentary beds with limited exposure along rivers and roadcuts in western Amazonia have provided a high diversity of vertebrate fossils of late Miocene age (Simpson and Paula Couto, 1981; Paula Couto, 1982; Frailey, 1986; Campbell, 1996; Bergqvist et al., 1998; Gaffney et al., 1998; Bocquentin and Melo, 2006; Campbell et al., 2006; Cozzuol, 2006; Kay and Cozzuol, 2006; Latrubesse et al., 2007, 2010; De Iuliis et al., 2011; Góis et al., 2013; Ribeiro et al., 2013; Prothero et al., 2014; Antoine et al., 2016, 2017; Kerber et al., 2016, 2017). The nomenclature and correlation of the relevant strata yielding the fossils in lowland Colombia, Peru, Brazil, and Bolivia, as well as their relationship to tectonic behavior of the central Andes Mountains, are actively described and elucidated (Campbell et al., 2001, 2006, 2010; Gingras et al., 2002; Wesselingh et al., 2002, 2006; Cozzuol, 2006; Latrubesse et al., 2007, 2010; Hoorn et al., 2010a, b; Mora et al., 2010), although there is considerable debate over the age and origin of the youngest deposits of western Amazonia. Many authors seem to agree that the youngest deposits, which comprise the Madre de Dios Formation in Peru and the Içá Formation in Brazil, overlie and are separated from the older Tertiary deposits that comprise the Ipururo Formation in Peru and the Solimões Formation in Brazil by the Ucayali Unconformity (Campbell et al., 2006). The base of the younger formation comprises the Acre Conglomerate (Campbell et al., 1985), from which have come diverse collections of vertebrate faunas of late Miocene age with taxa assignable to the Huayquerian South American Land Mammal Age (SALMA) and the Chasicuan SALMA. Some taxa seem to suggest an even older age, which would be concordant with the geologic history of the region.

Despite the diversity of Miocene mammals and the spectacular diversity of living bats (Chiroptera, Mammalia) in the western Amazon Basin, only a handful of bats are yet known as fossils from the region. Antoine et al. (2016) reported two bat taxa from upper Miocene deposits, as well as other bats in older rocks, in the lowlands of the western Amazon Basin in the extensive Paleogene–Neogene sequence

near Contamana, Peru. The late Miocene taxa included a free-tailed bat of the Family Molossidae (Mayoan SALMA), and a sac-winged bat of the Family Emballonuridae (Mayoan–Chasicuan SALMAs), both of indeterminate genus (Antoine et al., 2016). Farther to the south, in younger strata of the Madre de Dios Formation, Czaplewski (1996) reported an extinct species of bulldog bat, *Noctilio lacrimaelunaris*, and a molossid bat of indeterminate genus from the Acre River and Purus River, Peru, respectively, both thought at the time to pertain to the Huayquerian SALMA.

Screen-washing of a small sample of sedimentary deposits in 1995 at a locality along the upper Juruá River in Acre, Brazil (Campbell et al., 2006:fig. 1, locality 3, also known as RJ-95-2 and Natural History Museum of Los Angeles County [LACM] locality 6288; Fig. 1), yielded two late Miocene bat specimens from the Acre Conglomerate Member of the Içá Formation (= Madre de Dios Formation in Peru). Other small mammals recovered from the Acre Conglomerate at this same locality included two erethizontid rodents (Campbell et al., 2006:195) and nearly two dozen other rodent teeth, which are considered to be approximately equivalent in age to the Huayquerian vertebrate fauna from the Acre River and Purus River farther to the southeast. Elsewhere in western Amazonia, other Huayquerian taxa comprise mostly large mammals and do not yet include bats (Bergqvist et al., 1998; Negri et al., 2010; Ribeiro et al., 2013; Kerber et al., 2016, 2017).

The purpose of this paper is to describe two specimens of bats recovered from the Acre Conglomerate along the Juruá River, including a distinctive new taxon of disc-winged bat of the Family Thyropteridae. The previous record of Thyropteridae in the Neogene is limited to two taxa from the middle Miocene (Laventan SALMA) La Venta local fauna, Colombia (Czaplewski, 1997; Czaplewski et al., 2003).

METHODS AND MATERIALS

The Juruá River fossil teeth were compared with resin casts of Neogene fossil bats and museum specimens of modern bats of all families occurring in the western hemisphere (Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Phyllostomidae, Noctilionidae, Thyropteridae, Vespertilionidae). The Juruá River fossil teeth are clearly distinct from all bats except those belonging to the families Thyropteridae and Emballonuridae, thus the comparisons reported below are primarily with those two families. Dental terminology follows Legendre (1985), Sigé et al. (1994), and Kielan-Jaworowska et al. (2004:fig. 11.1). Measurements were made on an Olympus SZX9 stereomicroscope with an eyepiece reticle to the nearest 0.01 mm.

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Figure 1 Map of western Amazonia with LACM locality 6288 indicated. Thick yellow lines indicate international borders; thin white lines indicate departmental borders in Peru and state borders in Brazil. Inset figure of South America with orange square shows location of larger image.

Abbreviations: LACM, Natural History Museum of Los Angeles County; Ma, million years ago; SALMA, South American Land Mammal Age.

SYSTEMATICS

Order Chiroptera Blumenbach, 1779

Family Thyropteridae Miller, 1907

Genus *Amazonycteris* new genus

TYPE SPECIES. *Amazonycteris divisus* new species.

INCLUDED SPECIES. Monotypic.

ETYMOLOGY. For the Amazon Basin, and Greek *nykteris*, “bat.”

DIAGNOSIS. A small bat with molars approximately the size of those of *Thyroptera tricolor*. The M^1 differs from that of other thyropterids and from nearly all known insectivorous bats, except those of the family Emballonuridae, in having a shortened preparacrista and lacking a stylocone and parastyle. Differs from the M^1 of Neogene and extant members of Emballonuridae in lacking a parastyle on the mesiolabial corner of the tooth, in possessing a hypocone that occupies much of the center of the talon rather than a hypocone on the lingual margin of a deeply basined talon, and in having a strong lingual cingulum extending posteriad from the base of the protocone and continuous with the metacingulum.

Amazonycteris divisus new species

Figure 2

HOLOTYPE. Natural History Museum of Los Angeles County (LACM) 143512, left M^1 .

DIAGNOSIS. As for the genus.

TYPE LOCALITY. LACM 6288, Turtle Rock II, 09°16'37" S, 72°40'47" W; right bank of Juruá River, approximately 1.6 km

upstream from locality Pedra da Tartaruga of Simpson and Paula Couto (1981), State of Acre, Brazil.

HORIZON AND AGE. Upper Miocene Acre Conglomerate of Campbell et al. (1985), which is the basal horizon of the Içá Formation (= Madre de Dios Formation in Peru). Sample taken from a lens just above Ucayali Unconformity (Campbell et al., 2006) on a large slump block sliding into river. Matrix consisted of coarse sand with small clay pebbles and clay, a local facies of the conglomerate noted in several sections along this stretch of the Juruá River by Simpson and Paula Couto (1981). Although the slump block has presumably been swallowed by the river in the 21 years since the fossil was collected, the fossiliferous horizon is probably still present in the remaining cliff.

ETYMOLOGY. From Latin *divisus*, “cut, separated,” in reference to the Serra do Divisor/Sierra del Divisor, the low mountain range separating Peru and Brazil; the holotype was found very near the border between the two countries.

MEASUREMENTS. Anteroposterior length, 1.13 mm; transverse width, 1.57 mm.

DESCRIPTION AND COMPARISONS. Labial border of the tooth is markedly oblique, indicating the molar locus as M^1 . The tooth is unworn or very lightly worn. It bears a nonbasined talon of moderate size that extends linguad as far as the base of the protocone and distad to a level even with the metastyle. The tooth lacks an anterior lingual cingulum, but it exhibits a posterior lingual cingulum running between the base of the protocone and the talon. Posterior lingual cingulum is continuous with the talon cingulum, which in turn is continuous with the metacingulum. There are no cusps on the talon cingulum (postcingulum). The M^1 postprotocrista extends distad as a relatively strong ridge straight from the protocone apex, ending on a hypocone in the center of the talon. The postprotocrista lacks a rise in height along its length; its posterior terminus would be termed a “metaconule” by Fracasso et al. (2011), but we prefer to call it a hypocone. The M^1 commissures of the W-shaped ectoloph become progressively longer from preparacrista to postmetacrista. A paraconule is lacking, but there is a weak paraloph extending from the base of the paracone toward the protocone. There is a relatively strong, sinuous metaloph extending from the base of the metacone to the postprotocrista and closing off the trigon basin and protofossa posteriorly. Preprotocrista passes labiad from the protocone as a paracingulum, narrowing as it reaches the mesiolabial corner of the tooth. Preparacrista is short; stylocone and parastyle (“paracingulum expansion” of Fracasso et al., 2011) are absent. Mesostyle forms a curved ridge that is slightly elongated mesiodistally. Ectocingulum is indented by ectoflexi on either side of the mesostyle, and bears a small cusplule just mesial to the metastyle.

The M^1 of *Amazonycteris* resembles that of *Thyroptera*, previously the only known genus in the Family Thyropteridae, in most aspects of its morphology except for the mesiolabial corner of the tooth. The M^1 of *A. divisus* shares with that of *Thyroptera devivoi*, *T. discifera*, *T. lavalii*, *T. tricolor*, *T. wynneae*, and the La Venta *Thyroptera* spp. a nearly straight postprotocrista directed posteriad from the protocone; a small talon supporting a hypocone as a swelling beneath the posterior end of the postprotocrista; a short preparacrista; a weak paraloph; a metaloph directed toward the protocone and postprotocrista; a lingual cingulum developed at and posterior to the base of the protocone, and which is continuous with the talon cingulum and metacingulum; a preprotocrista continuous with the paracingulum and extending to the mesiolabial corner of the tooth; and a small ectocingular cusplule anterior to the metastyle. In terms of the M^1 , the known species of *Thyroptera* differ only subtly from one another in minor details of dimensions and morphology. In some individuals of *T. discifera* and *T. tricolor*, the lingual cingulum extends a short distance anterior to the base of the protocone, but in most, the lingual cingulum occurs only at the base of

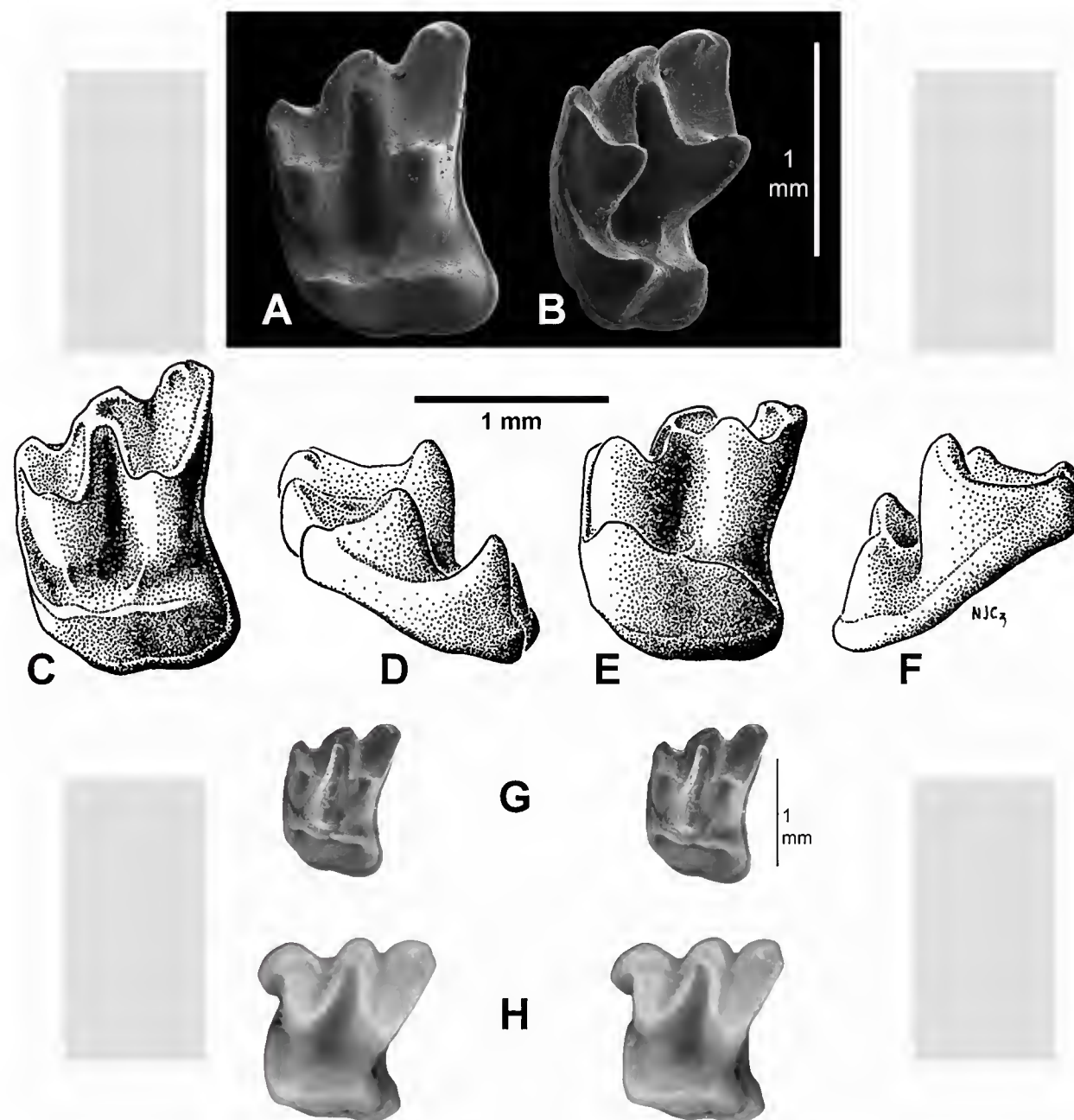


Figure 2 Thyropteridae, *Amazononycteris divisus* new genus and new species, left M¹ (holotype, LACM 143512) from the Juruá River, LACM locality 6288, State of Acre, Brazil; scanning electron micrographs in, A, occlusal and, B, oblique anterocclusal views; line drawings in, C, occlusal; D, anterior; E, lingual; and F, posterior views; G, stereopair, occlusal view. *Thyroptera tricolor*, H, stereopair of left M1 of a modern specimen for comparison.

the protocone and distally, as in *Amazononycteris*. *Amazononycteris* is distinct from *Thyroptera*, all species of which have a strong M¹ stylocone and parastyle, in having M¹ that lack these structures (compare Fig. 2G and H). The M¹ talon in *A. divisus* is a little better developed than M¹ talons in species of *Thyroptera*, in that it extends slightly farther distad and bears a slightly broader shelf along the distal edge of the tooth confluent with the metacingulum. In *Amazononycteris*, the posterior edge of the M¹ is less constricted distally, so that the talon occupies more area than in *Thyroptera* when seen in occlusal view.

As noted by Simmons et al. (2016), all bats, including archaic Eocene taxa, share dilambdodont tribosphenic molars, with the upper molars having a symmetric W-shaped ectoloph with a strong parastyle, as well as other characters; these characters are probably plesiomorphic for bats. The M¹ of *Amazononycteris* shows a symmetric W-shaped ectoloph, but it differs from the M¹ of almost all insectivorous bats, except those of species of the Emballonuridae, in lacking a parastyle and stylocone. All extant and Neogene Emballonuridae share derived characters of the M¹, in having a shortened preparacrista and lacking a stylocone, but retaining a parastyle (Storch et al., 2002). Paleogene European and Afro-Arabian emballonurids *Vespertiliavus* Schlosser, 1887, *Tachypteron* Storch et al., 2002, and *Dhofarella* Sigé et al., 1994, have a strong M¹ parastyle and often a weak to strong stylocone (*Dhofarella* M¹ has a tiny stylocone and a separate, prominent parastyle; Sigé, 1988; Sigé et al., 1994; Sigé and Menu, 1995; Storch et al., 2002). Despite the superficial resemblance of *A. divisus* to emballonurids, the *Amazononycteris* M¹

further differs from those of most emballonurids in having a lingual cingulum and in the size and shape of the talon. The M¹ talon in *Amazononycteris* is relatively smaller than that in all emballonurids. Unlike emballonurids, the M¹ talon in *Amazononycteris* and other thyropterids has no deep basin; it also has no separate, distinct, and lingually situated hypocone as in the Old World emballonurid genera *Saccolaimus*, *Taphozous*, *Coleura*, and *Emballonura*. Instead, *Amazononycteris* has the hypocone centrally positioned on the talon.

Family Molossidae Gervais, 1856

Genus and species indeterminate

Figure 3

REFERRED SPECIMEN. LACM 143509, right P₂, from locality 6288.

DESCRIPTION AND COMPARISONS. Bears two roots (one broken) that might have been partly coalesced. Shape closely resembles the P₂ of several molossid genera, including *Nyctinomops*, *Eumops*, *Molossops*, *Promops*, and *Mormopterus*. Size is much larger than the P₂s of *Mormopterus kalinowskii* and *Mormopterus phrudus*. It is smaller than the P₂ in *Promops nasutus*, *Molossops (Cabreramops) aequatorianus*, and *Nyctinomops laticaudatus*; much smaller and lower in crown height than P₂ of *Molossops greenhallii*; and much smaller than P₂ of the small *Eumops* species *E. patagonicus*, but very close in size and shape to P₂ of *Eumops bonariensis nanus*. Unfortunately, the P₂ is inadequate for referral to one of the above genera.

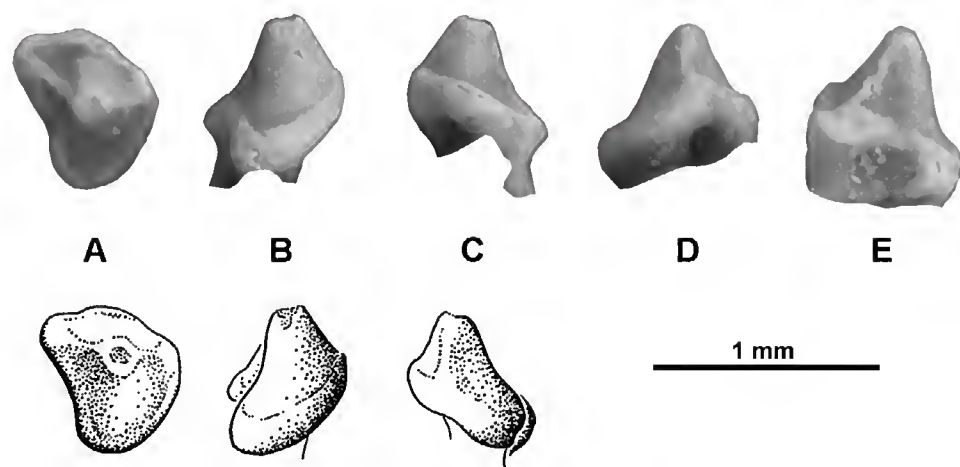


Figure 3 Molossidae, genus and species indeterminate, right P_2 (LACM 143509) from the Juruá River, LACM locality 6288, State of Acre, Brazil; photographs of ammonium chloride-coated specimen and line drawings in, A, occlusal views, mesial to right; B, labial views, anterior to right; C, lingual views; D, anterior view; E, posterior view.

MEASUREMENTS. Anteroposterior length, 0.62 mm; transverse width, 0.72 mm.

DISCUSSION

The known middle Miocene La Venta thyropterids consist of two taxa that were referred to the modern genus *Thyroptera*; one was comparable to an extant species and identified as *T. sp. cf. T. tricolor*, and the second was nominated as a new species, *T. robusta* (Czaplewski, 1996, 1997). At that time, only two species of *Thyroptera*, *T. tricolor* and *T. discifera*, were known, both extant. While the volume in which the article naming *T. robusta* eventually appeared was in press (Czaplewski, 1997), another extant species was named *T. lavalii* by Pine (1993). A re-examination and comparison of the available fossil teeth of the La Venta *T. robusta* with borrowed skulls of *T. lavalii* showed that the teeth of *T. robusta* were the same size and had the same morphology as comparable teeth in *T. lavalii*. Because it was not possible to negate the hypothesis that the two samples *T. lavalii* and *T. robusta* represented distinct species based on the few available teeth of *T. robusta*, Czaplewski (1996) synonymized *T. robusta* with *T. lavalii* (with the synonymization ultimately appearing before the La Venta volume did). Thus, both La Venta fossil thyropterids were tentatively referred to the modern species *T. tricolor* and *T. lavalii* pending the discovery of more complete fossil material. Since that time, two more extant species of *Thyroptera*, *T. devivoi* and *T. wynneae*, were named (Gregorin et al., 2006; Velazco et al., 2014). The cheek teeth are exceedingly similar among all five extant species of *Thyroptera* (*T. devivoi*, *T. discifera*, *T. lavalii*, *T. tricolor*, and *T. wynneae*), although the incisors differ in details. These species are differentiated mainly on characters of the skull and soft anatomy (Solari et al., 2004; Velazco et al., 2014). Up to four *Thyroptera* species co-occur in western Amazonia today (Velazco et al., 2014); this impressive local diversity within a single genus indicates clearly that they are ecologically and behaviorally more distinct than their conservative dental anatomy indicates. An investigation of the diet of *T. tricolor* indicates that the species is a specialized surface-gleaner, taking tiny, silent, often nonflying arthropods as prey (Dechmann et al., 2006); the foods eaten by the other species of *Thyroptera* are barely known.

A recent species-level time-calibrated phylogenetic analysis of all families of the superfamily Noctilionoidea placed Thyropteridae as the sister taxon to all other noctilionoid families except Mystacinidae (Rojas et al., 2016). The same authors estimated that thyropterids had diverged from other noctilionoids in the later Eocene and that the diversification of the recent species of *Thyroptera* had begun in the Miocene, by about 20 Ma. Few Neogene fossils of thyropterids are yet available to confirm

these divergences. The dental similarity among extant thyropterids and that between the extant thyropterids and the La Venta fossils, together with the middle Miocene age of the La Venta fossils, led Velazco et al. (2014) to suggest that the La Venta thyropterids could represent extinct taxa in which little dental evolution has occurred during the last 12 million years rather than long-lasting modern taxa as advocated by Czaplewski (1996) and Czaplewski et al. (2003). Velazco et al. (2014) suggested there was probably a hidden additional diversity in the Neogene fossil record of Thyropteridae but agreed with Czaplewski (1996) and Czaplewski et al. (2003) that more complete specimens would be necessary to demonstrate the extent of that diversity. They further correctly noted that the La Venta fossil bats indicate that the genus *Thyroptera* was distinct by 12.5 Ma, and that the teeth of the five recognized extant species of thyropterids lack many distinguishing characteristics. Reyes-Amaya et al. (2016) confirmed the similarity of the La Venta *T. sp. cf. T. tricolor*, at least in most dental measurements, to present-day *T. tricolor*, reinforcing the possibility of a long evolutionary stasis in that species' dentition. The present specimen of *A. divisus*, although geochronologically younger, is not represented by as many specimens as the La Venta fossil thyropterids. Its unusual morphology provides an unexpected glimpse at the late Neogene diversity of this family beyond the face value of the single available tiny tooth.

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